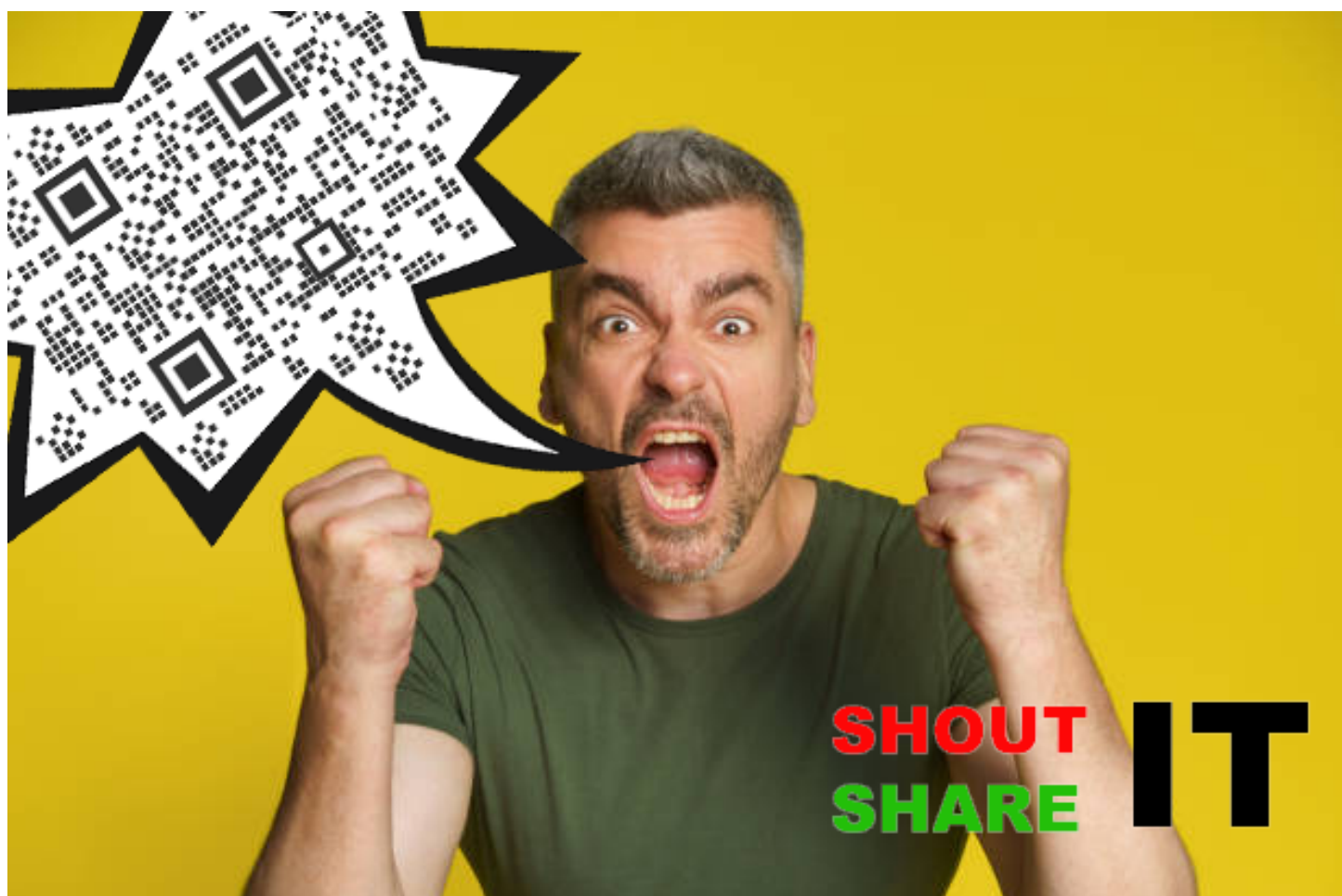
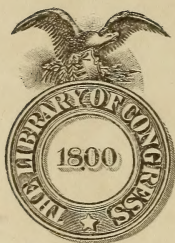


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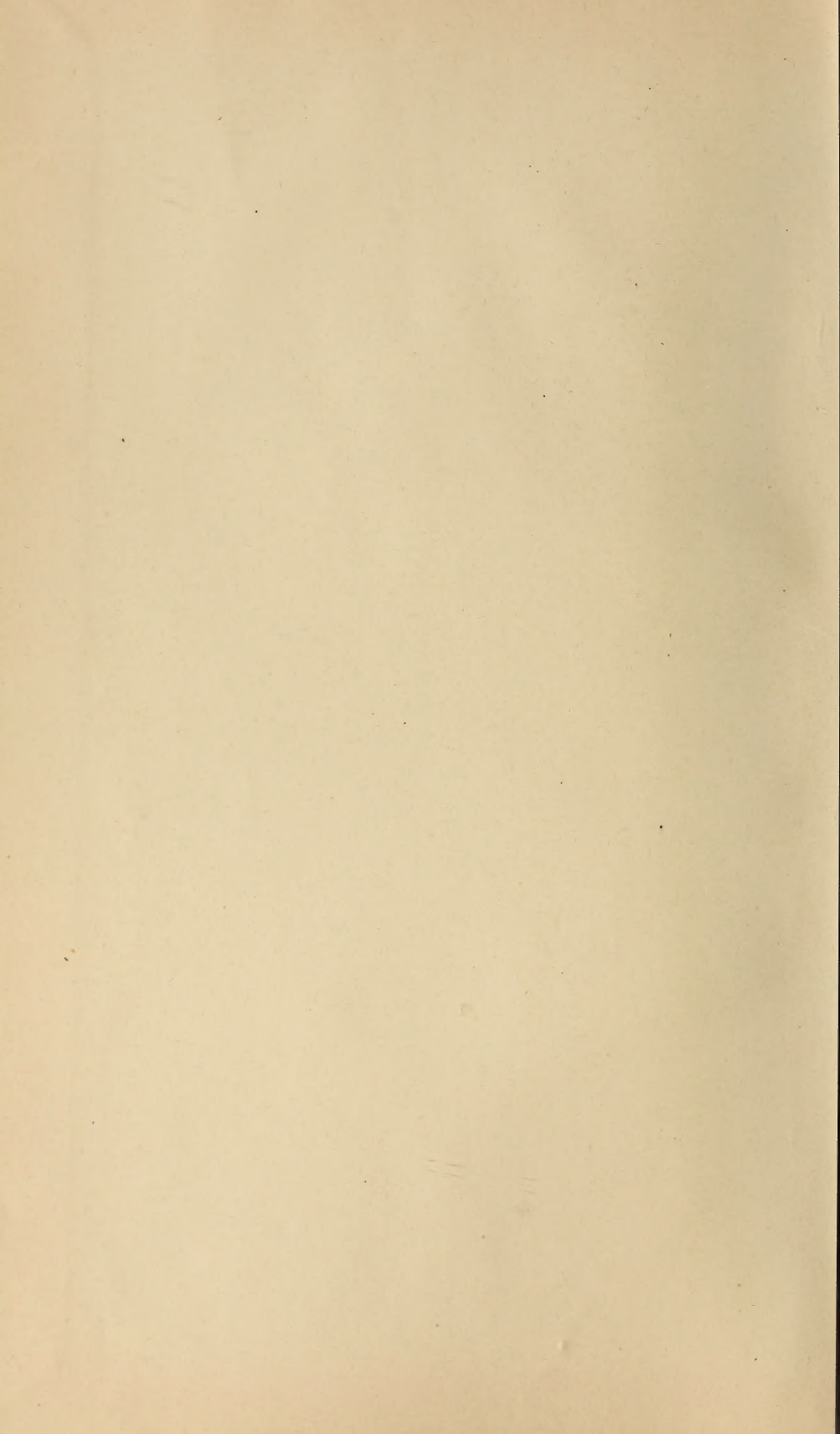
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BUREAU OF PLANT INDUSTRY—BULLETIN NO. 165.

B. T. GALLOWAY, *Chief of Bureau.*

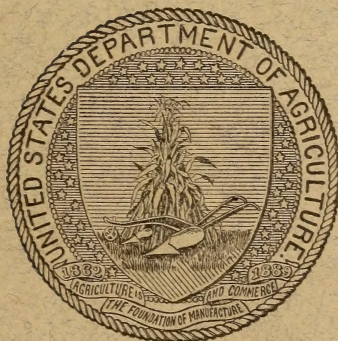
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BY

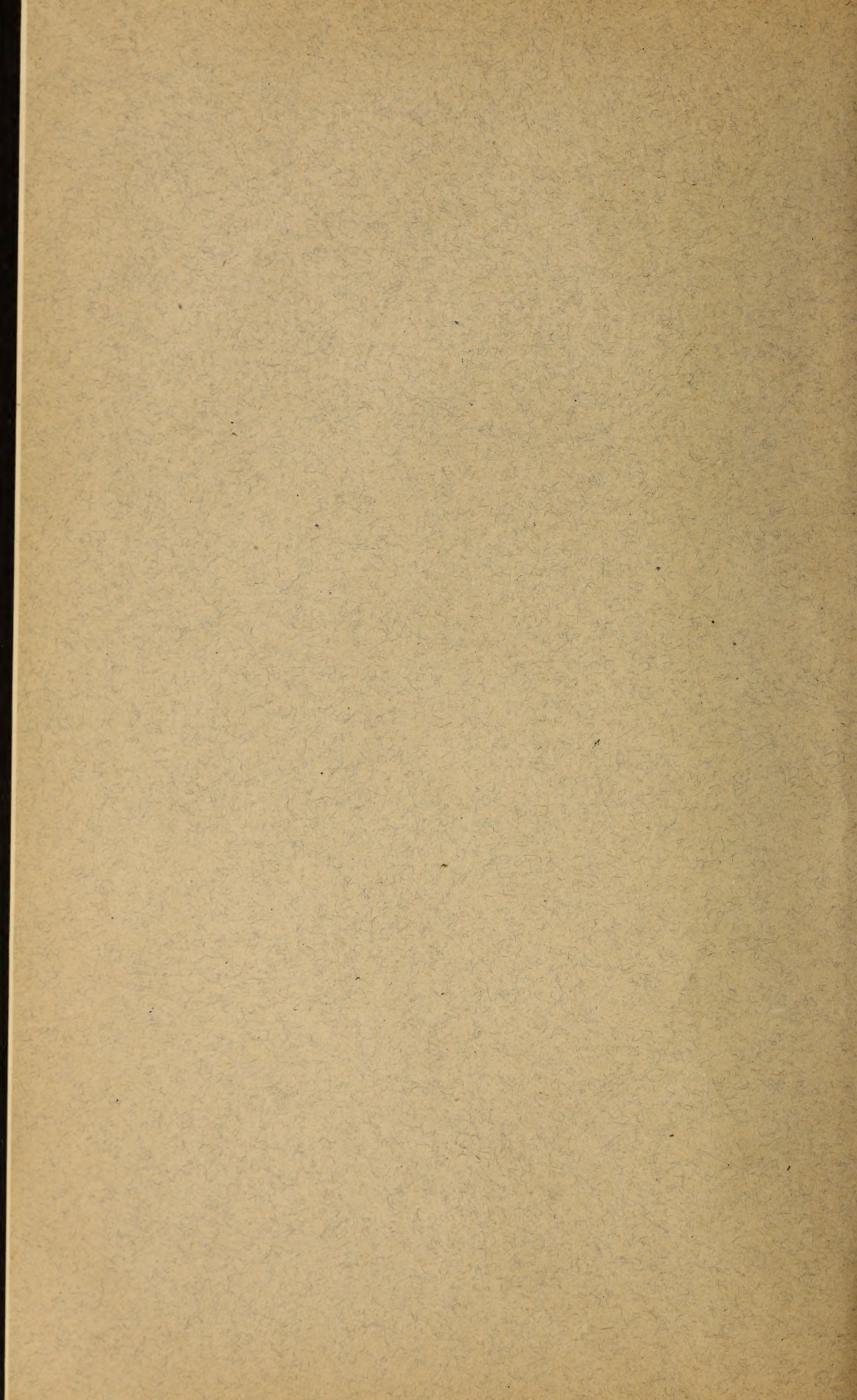
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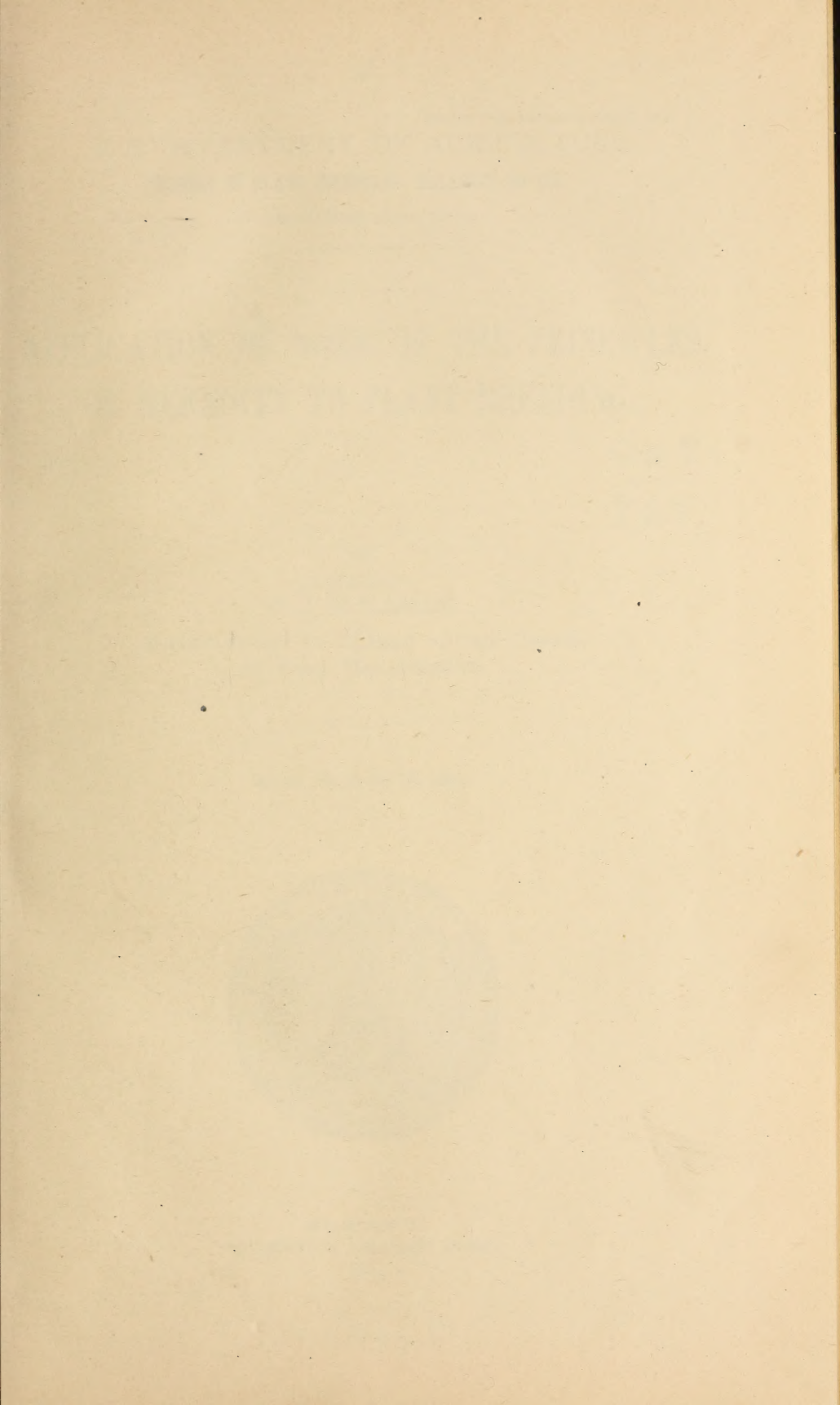
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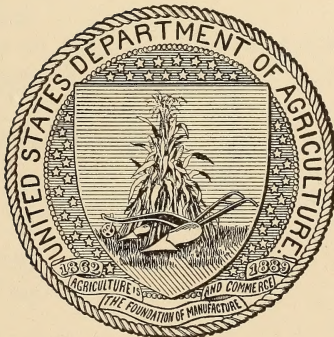
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BY

William J. Spillman
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LETTER OF TRANSMITTAL.

U. S. DEPARTMENT OF AGRICULTURE,
BUREAU OF PLANT INDUSTRY,
OFFICE OF THE CHIEF,
Washington, D. C., August 28, 1909.

SIR: I have the honor to transmit herewith and to recommend for publication as Bulletin No. 165 of the series of this Bureau the accompanying manuscript entitled "Application of Some of the Principles of Heredity to Plant Breeding." This paper was prepared by Mr. W. J. Spillman, Agriculturist in Charge of the Office of Farm Management of this Bureau. Great progress has been made during the past ten years in investigations relating to the principles involved in the improvement of plant varieties and the production of new varieties by cross-breeding. Thus far there has been no general statement of the principles applicable in this work especially designed for the use of the actual breeder. The present paper is an attempt to set forth in an orderly manner what is known of the effect of selection on different types of plants and the possibilities of cross-breeding for the purpose of producing new varieties, as understood by the author.

The paper is submitted and recommended for publication in accordance with the fixed policy of this Bureau of giving its men full opportunity of presenting results of scientific and practical interest from different points of view.

The author wishes to acknowledge the helpful criticism of Prof. C. V. Piper, and especially of Assistant Secretary Willet M. Hays, both of whom have carefully read the manuscript and have made many valuable suggestions in the treatment of the various topics.

Respectfully,

B. T. GALLOWAY,
Chief of Bureau.

HON. JAMES WILSON,
Secretary of Agriculture.

CONTENTS.

	Page.
Introduction.....	7
Dominance and recessiveness.....	7
Segregation.....	8
Allelomorphism.....	17
Law of recombination.....	18
Fluctuating variations.....	23
Running out of varieties.....	25
Selection without artificial crossing.....	26
Vegetative propagation.....	26
Self-fertilized species.....	32
Mass selection.....	33
Individual selection.....	35
Cross-fertilized species.....	36
Hybridization and selection.....	46
Vegetatively propagated crops.....	46
Self-fertilized species.....	47
Cross-fertilized species.....	53
Mendelian analysis of heterozygote races.....	54
Heterozygote characters.....	55
Possibility of entirely new characters.....	58
Reciprocal crosses.....	59
Evolutionary changes and their relation to plant breeding.....	59
Place effect.....	61
Non-Mendelian characters.....	62
Mutations.....	64
Latency.....	65
I. Latency due to separation.....	65
II. Latency due to dominance of absence over presence.....	67
III. Latency due to homozygosis.....	68
IV. Latency due to hypostasis (masking).....	69
V. Latency due to inhibition.....	69
VI. Latency due to fluctuation.....	69
Correlation.....	70
Index.....	71

ILLUSTRATIONS.

	Page.
FIG. 1. Graphic illustration of the range of fluctuations of each of the eight pure races of <i>Paramecium</i> studied by Jennings.....	28
2. Graphic illustration of ten generations of corn with no selection, the first generation of which is <i>Y₇Ss</i>	38
3. Graphic illustration of the effect of mass selection in cross-fertilized species.....	42
4. Graphic illustration of ten generations of a hybrid in a self-fertilized species without selection to type.....	50
5. Graphic illustration of ten generations of a hybrid in a self-fertilized species selected for type <i>WWCC</i>	52
6. Graphic illustration of the effect of individual selection in a self-fertilized species on progeny of the hybrid <i>WwCc</i>	53

APPLICATION OF SOME OF THE PRINCIPLES OF HEREDITY TO PLANT BREEDING.

INTRODUCTION.

While the discussion in these pages of principles that may be applied in the improvement of crops by breeding and selection will involve principles other than those discovered by Gregor Mendel, the fact that Mendel's principles are somewhat complex renders it necessary to state them in a general way before taking up the subject of plant improvement.

DOMINANCE AND RECESSIVENESS.

The simplest of the principles discovered by Mendel is that which is usually referred to as the "law of dominance." This principle should hardly be called a law, because it is in no wise general and in very few cases is dominance absolute. The phenomena of dominance and recessiveness may be illustrated by a few examples.

If a red-flowered variety of the common garden pea be crossed with a white-flowered variety, the progeny will have red flowers. According to Mendel's original conception a cross of this kind brings together two antagonistic characters. The progeny inherit the red flower color from one parent and the white flower color from the other. It therefore has both these characters. It happens, however, that the red character predominates over the white and comes to expression while the white character is not visible in the cross-bred individual. Mendel suggested that a character behaving as the red character does in this cross should be called a "dominant character," while one behaving as the white character in this cross should be called a "recessive character."

If we cross a bearded variety of wheat with a smooth variety, that is, one that has no beards, the hybrids thus produced either have no beards or the beards will be only slightly developed. Hence, we say that smoothness is dominant to beards, at least partially, or, which means the same thing, that beards are recessive to smoothness. The cross between polled and horned breeds of cattle has no horns, though a small proportion of such cross-bred animals may have "scurs,"

that is, imperfect horns. Hence, we say that horns are recessive and the poll character dominant. Many other cases might be cited to illustrate dominance and recessiveness of hereditary characters, but the above examples will serve to illustrate the principles sufficiently here.

While it is not uncommon for a character to be dominant or recessive in a cross, it is seldom that dominance is absolute. The presence of the recessive character can usually be detected, and in some cases very easily. Thus, in the cross between bearded and smooth wheat the hybrids usually show a slight tendency to be bearded. Likewise, as already stated, the cross between horned and polled cattle may have scurs. It frequently happens that instead of either of two opposite characters being dominant we get a form intermediate between the two parent forms. Thus, in the cross between ordinary long-headed wheat and the short-headed club wheats of the Pacific coast the hybrid has heads of intermediate length, though they are much more like club wheat than they are like the ordinary kinds, so that the club character is at least partially dominant. In certain crosses between red-flowered and white-flowered ornamental plants the hybrids are pink.

In not a few instances a hybrid is altogether different in some characters from either of its parents. Thus, in the case of the cross between a certain red primrose and a certain nearly related white variety the hybrid is purple.

We thus have every gradation between perfect dominance of a character over its opposite and cases in which the hybrid is unlike either parent.

SEGREGATION.

We have seen that when two naturally opposite characters meet in the same individual one of them may be completely dominant, as the poll character in many individuals of the cross between polled and horned cattle, or the crossbred individual may exhibit a character intermediate between the opposed characters of its parents, as the pink color of certain hybrids between red-flowered and white-flowered plant varieties, or the hybrid may exhibit a character different from the corresponding characters of either of its parents, as the purple color of hybrid primroses produced by crossing certain red and white varieties.

In a pure race of plants having red flowers we may assume that each individual which bears seed transmits to all its seed the tendency to produce red flowers. Likewise, in a pure white-flowered race, each individual transmits to its progeny the tendency to produce white flowers. But what of the hybrid between two such

racess? What does this hybrid transmit to its offspring? Let us consider the case of the hybrid primrose having purple flowers. The facts are, as found by experiment, that this purple hybrid produces three kinds of progeny. About one-fourth of the seed produced by this hybrid produces plants having red flowers like those of the red-flowered parent of the hybrid. Another fourth have white flowers, while the remaining half have purple flowers. Furthermore, the red and the white flowered plants of this second generation will reproduce only red or white progeny, as the case may be; that is, they behave exactly like pure red or pure white races. On the other hand, every one of the purple-flowered plants will produce in the next generation three kinds of progeny as before. One-fourth of the progeny of these purple-flowered plants will have red flowers, one-fourth of them white flowers, and half of them purple flowers. This experiment was continued by an English florist for fifteen years, always with the same result. The purple always split up into one-fourth red, one-fourth white, and one-half purple, while the reds and the whites thus produced always behaved like pure races of red or white. From these facts we infer that in self-fertilized species an individual which is hybrid with reference to a particular pair of characters tends to produce progeny one-fourth of which is of pure race like one of the parents of the hybrid, another fourth of pure race like the other parent, while the remaining half is hybrid like the original hybrid itself.

Mendel suggested that the cause of these peculiar phenomena is that the hybrid produces two kinds of ovules and two kinds of pollen, the one kind of ovule and one kind of pollen being exactly like those of one of the parents of the hybrid so far as the one character under consideration is concerned, the other kind being like those of the other parent. Let us see how this hypothesis fits the facts.

Suppose the hybrid does produce two kinds of ovules in equal numbers, one of which carries the potentiality of the red flower color, the other that of the white, and two kinds of pollen differing in a similar manner. Let us designate the ovules and pollen carrying red by the letter *R*, and those carrying white by *W*. Let us first consider what happens to the ovules of type *R*. These ovules are offered both *R* and *W* pollen in equal quantities. The chances are, therefore, that half the *R* ovules will be fertilized by *R* pollen and the other half by *W* pollen. In the first of these cases, we have *R* ovules fertilized by *R* pollen, which would, of course, give pure red individuals. For convenience, we may designate these individuals resulting from the fertilization of *R* ovules by *R* pollen as *RR* individuals. Since half of the ovules produced by the hybrid are supposed to be of type *R* and since half of these are fertilized by *R*

pollen it follows that one-fourth of the progeny of the hybrid will be pure reds. Similarly, the *W* ovules are offered both kinds of pollen, and the chances are that half of these ovules, or about half, will be fertilized by *R* pollen, the other half by *W* pollen. The latter half being fertilized by pollen of their own kind result in pure white individuals, which we may, for convenience, designate as *WW* individuals, thus indicating that both the ovules and the pollen which gave rise to these individuals had the character *W*. The *WW* individuals also constitute one-fourth of the progeny of the hybrid. The remaining half of the progeny result from the fertilization of one kind of ovule by the opposite kind of pollen, thus giving hybrids like the original hybrid, which we may designate by the formula *RW*.

We thus see that the supposition that the hybrid produces two kinds of pollen, one like the pollen of the red variety and the other like that of the white, and two kinds of ovules, differing in a similar manner, fully explains the phenomena observed by the breeder of the purple primrose. This hypothesis is further substantiated by the following facts. If we apply the pollen of the hybrid to the stigmas of the red variety, half the progeny thus obtained will be red and half purple. This is easily understood if the hybrid produces two kinds of pollen in equal quantities. All the ovules of the red variety have the character *R*. If half the pollen of the hybrid carries *R*, then half the progeny will be *RR*, or pure red. If the other half of the pollen carries *W*, then the other half of the progeny will be of the type *RW*. That the hybrid produces two kinds of ovules is shown also by the fact that if we apply pollen of the red variety to the stigmas of the hybrid, half the resulting progeny will be red and half purple.

We may accept the hypothesis, therefore, that a hybrid plant whose parents differ in respect to a single character pair produces two kinds of ovules and two kinds of pollen, one kind being like those of one of its parents, the other kind like those of its other parent.

If a hybrid which has in its cells two characters which are naturally the opposite of each other can not produce ovules and pollen with both of these characters in the same ovule or pollen grain, then it follows that these two opposite characters can not be transmitted together. They remain together in the cells of the hybrid well enough, but they fall apart somewhere in the process of producing reproductive cells. Let us now inquire how this segregation of the members of a pair of opposite characters into different ovules and different pollen grains, which takes place in hybrids, may occur. In the cells of a plant we have, first, the outer covering, or cell wall. Within is the nucleus, between which and the cell wall lies the

cytoplasm, consisting of a semi-liquid ground substance, in which lies the network of the cytoplasmic reticulum, in the meshes of which occur various small bodies called collectively the cytoplasts. Within the nucleus, which is separated from the cytoplasm by the nuclear membrane, are found the chromosomes, which are small bodies of living substance lying in the nuclear sap or ground substance of the nucleus. We must seek for the potentialities of the hereditary characters either in some of these cell organs or in their relations to each other. The behavior of the chromosomes is such as to suggest strongly that they are the seat of at least some of the potentialities in question. The work of Prof. E. B. Wilson and his pupils and others indicates that in certain animals certain identifiable chromosomes are responsible for the differences between the sexes, at least for the primary sexual differences. Several other hereditary characters not directly related to sex behave in such manner as to indicate clearly that they bear to the chromosomes a relation similar to that which sex bears to these cell organs. It is highly probable, therefore, that many hereditary characters depend in some way not yet understood on the chromosomes. In fact, when we describe the known behavior of the chromosomes we describe the known behavior of Mendelian characters.

It is not necessary in this discussion to consider the various theories regarding the relation of hereditary characters to the organs of the cell. The behavior of the characters studied by Mendel and of hundreds of characters investigated by others leaves no doubt that these characters depend in some way on definite cell organs. This does not necessarily imply that each hereditary peculiarity of a race is represented by a distinct body in the germ cells. A given peculiarity may be due to peculiarities in the composition or the physiological behavior of several cell organs. This much, however, seems to be certain: When two races differ in respect of a character and when the hybrid between these races produces two kinds of reproductive cells, one of which is like the reproductive cells of one of its parents and the other like those of the other parent, as is the case in primroses just cited, then the difference between these two races is due to differences in a single cell organ or to a group of such organs which act together at all times as if they were inseparable. In hybridization we are dealing with differences between organisms, and these differences are due to differences between corresponding cell organs in the different races. For instance, suppose we have two races of plants which differ only in the fact that one of them has red flowers and the other white and that the hybrid between them produces two kinds of pollen, one of which is identical with the pollen of the red variety and the other with that of the

white variety. We know that the real difference between these varieties lies in the fact that one of them produces red coloring matter and the other does not. We may therefore assume that in the white variety a certain cell organ fails to perform a function which the corresponding organ in the other variety does perform. We may call this function which is performed in the red variety the "determiner" for red. In the white variety this determiner is absent, although the cell organ which performs this function in the other variety may be present in the white variety. In this variety it fails to perform the function necessary to the production of red coloring matter.

We should not get the idea that red coloring matter is due wholly to a single function of a single body, for such is probably not the case. It may be necessary for several cell bodies to cooperate in the production of this substance. In the white-flowered variety all of these bodies may function properly except one, the failure of the one body to perform its appropriate function being responsible for the nonproduction of the red coloring matter. But when we are dealing with a cross between these two varieties it is the one point in which they differ that concerns us, and we shall use the word "determiner" to apply to this point of difference. Hence, we say that in the one variety the determiner for red is present and in the other it is absent.

Although the determiner of a character is assumed to be a function of a definite body, or of several such, we shall not attempt in what follows to distinguish in all cases between these bodies and their functions. In general, we shall represent the determiner for a character by a capital letter, usually the initial letter of the name of the character. Thus, capital *R* may be taken as the symbol of the determiner for red coloring matter, but this symbol will be used indifferently for the function which produces red and for the body or group of bodies which has this function. For the absence of this determiner in the white variety we shall use the corresponding small letter. Thus, *r* may be considered in what follows as representing the absence of the function *R*, or it may be considered to represent the body present in the white variety that fails to perform the function which is performed by the corresponding body in the red variety.

We are now ready to explain why the hybrid between a red and a white variety of primrose produces two kinds of reproductive cells, one like those of the red variety and one like those of the white—at least, to offer an hypothesis that agrees with the facts.

The red variety has inherited the determiner for red from two parents. The condition of this determiner in the red variety may

therefore be represented by the symbol RR . This means that in the cells of a plant of the red variety there are two determiners for red. The corresponding determiners in the white variety may be represented by the symbol rr , which may be taken as representing two bodies, neither of which performs the function necessary to the production of red coloring matter, but which correspond in the white variety to homologous bodies which do perform this function in the red variety. The symbol of the hybrid would, of course, be Rr , in which R represents the "active" determiner derived from the red variety and r the nonactive one from the white variety. In ordinary growth, when a body cell has attained its maturity and divides into two cells it is supposed that each character determiner present divides, one part going into one of the new cells, the other into the other. Thus, if a mature cell contains the determiners R and r , then each of the new cells formed by its division likewise contains both R and r . Thus every cell in the body of the individual may be supposed to have both R and r in it. This is certainly true of those cells which form the direct line of descent from the original fertilized ovule to the new ovules and pollen grains produced by the individual. The cells in this line of descent are called collectively the germ cells, a term which we shall find convenient to use.

If ovules and pollen cells were formed by ordinary cell division such as that described above, it is clear that every ovule and every pollen grain produced by the hybrid Rr would contain both R and r . But the facts indicate that only half the ovules and half the pollen grains contain R , while the other half contain r . There must be, then, a cell division somewhere in the line of descent which differs from the ordinary type of cell division, and there is unmistakable cytological evidence that such is the case. Just before the formation of ovules and pollen grains (in fact, in next to the last division of the germ cells) we find a cell division in which the chromosomes do not divide in the usual manner. Instead they unite in pairs, forming double, or bivalent, chromosomes. This union of chromosomes into pairs reduces the number of chromosomes to half what it was before. Then, when the cell divides, these large chromosomes divide, presumably into the two halves which united to form them. If we call the large double chromosomes mother chromosomes and the small ones into which they separate daughter chromosomes, then in this cell division one of the daughter chromosomes passes to one of the newly formed cells, while the other passes to the other cell. Now, if these chromosomes either themselves are the bodies whose functions are our "determiners," or if they contain smaller bodies which are responsible for the determiners, we have at once an explanation of the fact that our hybrid produces two kinds of

ovules and two kinds of pollen. For in this cell division, which is called the reduction division because in it the number of chromosomes is reduced by half, our determiners R and r may be assumed to reside in separate chromosomes which unite to form a single bivalent. While cell division is taking place this bivalent chromosome again separates, R passing into one daughter cell and r into the other. If the determiners R and r are not simply the functions of chromosomes themselves they at least pertain to bodies which at some point in the line of descent of the germ cells behave just as we know the chromosomes do behave—that is, at some cell division R and r unite into a pair, and when division occurs R goes one way and r the other. Two determiners which thus behave toward each other are said to constitute a Mendelian pair.

Most Mendelian pairs consist simply of the presence of a given determiner on the one hand and the absence of that determiner on the other. Furthermore, the determiner which represents the presence of a character is in nearly all cases dominant over the determiner which represents the absence of that character. Dr. C. B. Davenport, of the station for experimental evolution of the Carnegie Institution, found that in poultry practically all the character pairs known show this relation; i. e., presence of a character dominant and absence of it recessive. We have seen, however, that there are some exceptions to this rule, since the poll character is dominant to horns and beardlessness in wheats is dominant to beards. The difference between polled and horned cattle is the absence of horns in one and their presence in the other.

But cases are known in which this simple relation of presence and absence of a character does not constitute the Mendelian pair. For instance, if Barred Plymouth Rock females be mated with Indian Game males all the female progeny of this mating will be black, while all the males will be barred like the mother. Data accumulated by the writer and an extended series of experiments performed by Mr. H. D. Goodale^a indicate that the female Barred Plymouth Rock produces two kinds of eggs. One of these kinds is destined to produce females, and these female-producing eggs do not have the determiner for barring in them. The other kind is destined to produce males, and these eggs do have the barring factor. In this case it appears, therefore, that the determiner for femaleness and that for barring form a Mendelian pair. Wilson has apparently shown that the determiner for femaleness in many animals is a certain chromosome or group of chromosomes that always act as a unit. If we assume that the determiner for barring is another chromosome which unites with the sex element to form a bivalent in the reduction division we have at once an explanation of the behavior of the determiner for barring. In the

^a See Science, June 25, 1909.

germ cells of the female Barred Plymouth Rock we have the two elements F , which causes the individual to be a female, and B , which gives the barring on the feathers. In ordinary cell division both of these elements divide; but in the reduction division F and B unite into one body. This body then separates as the cell divides, so that one of the daughter cells contains F and the other B . Such a female therefore produces two kinds of eggs, one containing the determiner for the female sex, the other that for barred feathers.

Several other cases are known in which Mendelian pairs are formed of determiners for characters that are apparently unrelated. Such a case occurs in the purple primrose previously mentioned. We may explain the phenomena presented by this hybrid as follows: Let us assume that the original wild species from which the red and the white races in question are descended had purple flowers and that this purple color was due to two functions of the same cell organ. One of these functions, which we may designate as R , had to do with the production of red coloring matter, while the other, which we may designate as P , changed red into purple, somewhat after the manner in which an alkali changes litmus from red to blue.^a The determiners R and P were functions of the same cell organ, probably a chromosome. Since this body had two functions we may represent it by the symbol $R-P$, the hyphen indicating that the two functions belong to the same cell organ. Since there is a pair of these bodies in each cell, the complete status of these determiners in the body cells would be represented by $R-P R-P$.

Now, let us suppose that in one section of the species the determiner R becomes latent or is lost. Our formula then becomes $r-P r-P$, or simply PP in this race, which would, of course, have white flowers, since the determiner for red is absent. In another section of the species the determiner P vanishes, leaving $R-p R-p$ or simply RR . Now, when we cross these two races we bring the determiner $r-P$ into the same cell with $R-p$. Here we have the red coloring matter produced by one determiner and converted into purple by the other. This would account for the purple color of the hybrid, as well as the red of one variety and the white of the other. Other cases of Mendelian pairs of this nature will be mentioned later.

In this purple hybrid we may consider that we have one character pair consisting of R from the red parent and r from the white parent, so that this pair consists of red and absence of red, while along with it we have another pair consisting of P from the white parent and p from the red parent, so that this pair consists of the presence of P and the absence of P . But the fact that P and R can not be transmitted together indicates that R and p pertain to the same

^a See article by Shull in American Naturalist, July, 1909.

cell organ, and that r and P pertain to the Mendelian mate of this organ. Since most Mendelian character pairs consist of determiners one of which represents the presence of something and the other the absence of the same thing, we shall, in general, use for such pairs of characters in hybrids symbols consisting of a capital letter and the corresponding small letter, the capital letter standing for presence of the character and the small letter for its absence. Thus, in the cross between red and white peas, since the difference between these varieties consists in the presence of red color in one and its absence in the other, we represent the hybrid as Rr . Since the hybrid itself is red in this instance, this formula is logical; it would naturally be red because of the presence of R . But, as previously stated, there are cases in which the absence of a character is dominant in the hybrid between races one of which has the character and the other does not. Thus the hybrid between polled and horned cattle is polled. Here the formula for the horn determiner in the pure horned breed would be HH ; in the pure polled breed, hh ; and in the hybrid, Hh . But since the determiner H does not succeed in producing horns in the hybrid and the hybrid therefore has the appearance of its polled parent we may write the formula for the hybrid as $(H)h$, to show these facts. Similarly, the hybrid between bearded and smooth wheat would be represented by $(B)b$.

Cases like the purple hybrid primrose are so rare that we do not need to use any particular symbol to indicate that the hybrid is unlike either parent.

The question why these characters, horns in cattle and beards in wheat, do not develop when represented by only one active determiner is an interesting one, and is very ably discussed by Doctor Shull in the July, 1909, number of the American Naturalist. The fact probably is that in these hybrids the determiners H and B are not latent, but that single determiners are not able to produce that chemical condition in the cell which is necessary for the development of these characters. In pure horned cattle and pure bearded wheat, where there are two active determiners for each of these characters, the proper condition for the development of these characters is brought about.

In general, a hybrid produces three types of progeny with reference to each pair of characters in which its parents differ. The hybrid between red and white varieties of peas produces two kinds of pollen, which we may designate as R pollen and r pollen. It produces two corresponding types of ovules. On the average, half the R ovules are fertilized by R pollen, so that one-fourth of the progeny of such a hybrid is of the type RR or pure red. Likewise, half the r ovules are fertilized by r pollen, giving rr individuals, which consti-

tute one-fourth of the second generation. The remaining half of the R ovules meet r pollen and the remaining half of the r ovules meet R pollen, giving in each instance the combination Rr , which constitutes half the second generation. If R is completely dominant the types RR and Rr can not be distinguished, since the latter has red flowers like those of type RR . Hence, where dominance is complete the second generation appears to consist of only two types. One of these types shows the dominant character, the other the recessive character, and the dominant type is three times as numerous as the recessive. Thus we arrive at the well-known Mendelian ratio of 3:1, or three dominants to one recessive in the second generation of a hybrid.

In the above second generation the two types RR and rr are seen to consist of like things united, while the type Rr consists of unlike things united. Types RR and rr are said to be homozygote, a term which means "like things united," while Rr is said to be heterozygote, which means "unlike things united." An individual is said to be homozygote with reference to a given character when the cells of that individual contain two determiners for the presence of that character. If its cells contain only one determiner for any character it is said to be heterozygote for that character. Thus a bearded wheat is homozygote for beards, a pure race of smooth wheat is homozygote for absence of beards, while a cross between a bearded and a smooth race is heterozygote for beards.

ALLELOMORPHISM.

The term "allelomorph" was introduced by Prof. William Bateson, of Cambridge, England, one of the leading investigators of Mendelian phenomena. It is derived from two Greek words, one of which means "one another" and the other "form." We may say that it means "corresponding forms." What we have called a "pair of determiners" Bateson calls a "pair of allelomorphs." The term "allelomorph," however, has a wider application than "determiner;" it may mean characters themselves as well as the determiners of those characters. To say that one character is allelomorphic to another means simply that the two characters when brought together in the same individual form a Mendelian pair and hence fall apart when reproductive cells are produced. Thus, a pair of allelomorphs is what we have been calling a "pair of Mendelian characters." Hence, the term "allelomorph" is frequently used simply to mean a Mendelian character; that is, a character which obeys Mendel's law of segregating from its mate in the reduction division.

The term "gamete" is also a very convenient one which we shall have occasion to use frequently. It simply means a reproductive cell, such as an ovule, a pollen grain, an unfertilized egg, etc.

LAW OF RECOMBINATION.

The third and most important principle discovered by Mendel^a is the fact that, generally speaking, when two or more "pairs" of characters are present in the same hybrid these pairs are independent of each other, so that one member of a given pair may be transmitted with either member of another pair. The results of this important discovery are shown in Table I, which illustrates the cross between Polled Durham and Hereford cattle.

As is well known, Polled Durham cattle have colored faces and no horns, while Herefords have horns and white faces. The white face of the Hereford seems to be due to the presence of a determiner which controls the distribution of color over the body. We thus represent white face by *W* and colored face by *w*, that is, absence of white face. As before, the poll character is represented by *h* and the horn character by *H*. White face is dominant to colored face in this cross. The complete formulæ for these two pairs of characters in the body cells are, therefore—

In pure Hereford cattle, *HHWW*.

In Polled Durham cattle, *hhww*.

In the cross, (*H*)*hWw*.

The cross has the white face but no visible horns, though it may have scurs.

The squares in the upper part of Table I represent germ mother cells dividing in the reduction division. In this division each pair of characters is separated. Thus, the pair *Hh*, both members of which have been present in every cell of the body of the hybrid, is here separated, *H* going to one daughter cell and *h* to the other. In the cross here under consideration we have a second pair of allelomorphs, namely, *Ww*. When a given mother cell divides, the two pairs of allelomorphs may be arranged as in the left-hand square at the top of Table I, in which case *H* and *w* go together into one daughter cell, while *h* and *W* go into the other. Such a division gives two kinds of gametes, the formulæ for which are, respectively, *Hw* and *hW*.^b Or the two pairs of allelomorphs may be arranged as in the right-hand square of Table I, in which case *H* and *W* go to the same daughter cell, while *h* and *w* go to the other, giving two kinds of gametes having the respective formulæ *HW* and *hw*. There are, in all, therefore, four

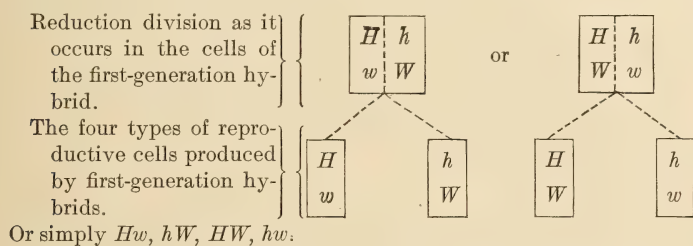
^a The first is the so-called "law of dominance," though it is hardly entitled to rank as a law; the second is the law of segregation of character pairs.

^b The gametic formula *Hw* does not represent a pair of determiners. It represents two determiners, one of which is from one pair and the other from another pair. We do not have pairs of determiners in gametes, i. e., in reproductive cells. The pairs separate in the reduction division, and a gamete never has both members of the same pair.

kinds of gametes that a hybrid individual of the type here under consideration can produce, namely, Hw , hW , HW , and hw . In the first of these four types of gametes, namely, Hw , we find horns being transmitted with colored face; in the third, HW , horns and white face are transmitted together. Likewise, in the second type, hW , we have the poll character and white face together, while in type four, hw , we have the poll character and colored face.

Since in the reduction division either of the two possible arrangements of the two pairs of allelomorphs is just as likely to occur as the other, one of them will occur in about half the cells and the other in the other half. We thus get all four types of gametes in equal numbers in every hybrid animal of this character. In the male this is actually realized, for millions of gametes are produced. But in the female only a few reproductive cells are formed, but these few are as likely to be of one type as another. Hence, on the average for a large number of such females, the four types of gametes will occur equally often. In the middle part of Table I we have all the possible, and equally probable, unions that can occur between the gametes of the two sexes. Thus the Hw gametes of the female are offered four kinds of sperm in equal numbers. Hence, on the average one-fourth of these Hw ovules will be fertilized by Hw sperm, giving individuals of the next generation of the type $HHww$. Another fourth will meet hW sperm, giving individuals of the type $(H)hWw$, and so on.

TABLE I.—Cross between Polled Durham and Hereford cattle and its results.



The sixteen possible, and equally probable, matings to produce second-generation hybrids are as follows:

Gametes of male.

Gametes of female.		Hw	hW	HW	hw
	Hw	1 $HHww$	2 $(H)hWw$	3 $HHWw$	4 $(H)hww$
	hW	5 $(H)hWw$	6 $hhWW$	7 $(H)hWW$	8 $hhWw$
	HW	9 $HHWw$	10 $(H)hWW$	11 $HHWW$	12 $(H)hWw$
	hw	13 $(H)hww$	14 $hhWw$	15 $(H)hWw$	16 $hhww$

The nine different combinations and their relative frequency follow:

1 <i>HHWW</i> .	2 (<i>H</i>) <i>hWW</i> .	1 <i>hhWW</i> .
2 <i>HHWw</i> .	4 (<i>H</i>) <i>hWw</i> .	2 <i>hhWw</i> .
1 <i>HHww</i> .	2 (<i>H</i>) <i>hww</i> .	1 <i>hhww</i> .

The sixteen formulæ in the squares in the middle of Table I show the results of these sixteen unions. It will be seen that some of these matings are alike; for instance, 2, 5, 12, and 15; 3 and 9; 4 and 13. There are only nine different kinds, as shown in the lower part of Table I. These nine different combinations occur in the relative frequencies shown in the numbers preceding each of the nine in the lower part of Table I. Thus, one-sixteenth of the progeny will represent the combination *HHWW*, four-sixteenths the combination (*H*)*hWw*, and so on.

Table II shows the results of a more complex cross which the writer made while connected with the Washington Agricultural Experiment Station, Pullman, Wash. It is a cross between two varieties of wheat, one of which was a winter wheat that lodged easily (that is, had weak straw) and had open chaff, and thus when ripe shattered its grain easily. The other was a variety of spring wheat that did not lodge and had tightly closed chaff when ripe. The first generation^a of the hybrid inherited a very complex lot of characters. Thus, it inherited both winter and spring character; both the lodging and the nonlodging tendency; both the open and the closed chaff tendency. In this cross the winter character, the nonlodging tendency, and the closed-chaff tendency were dominant.

Letting—

W stand for the winter character,
w for absence of winter character (i. e., spring character),
N for nonlodging (i. e., for stiff straw),
n for absence of *N* (i. e., for weak straw),
C for closed chaff, and
c for absence of *C* (i. e., for open chaff),

the formula of the hybrid was *WwNnCc*. Now this hybrid can produce, and does produce, in about equal numbers eight different types of ovules and eight similar types of pollen, namely, *WNC*, *WNc*, *WnC*, *Wnc*, *wNC*, *wNc*, *wnC*, *wnc*. The union of these eight types of ovules and pollen grains gives sixty-four possible, and equally probable, matings. But, as before, some of these matings give identical

^a Professor Bateson uses the symbol F_1 for first-generation hybrids. The *F* is the initial letter of the word "filial." Hence this symbol means "first filial generation." Bateson denotes the second and later generations of a hybrid by F_2 , F_3 , etc. Likewise, he denotes parental generations as follows:

P_1 =parents of the hybrid.
 P_2 =grandparents of the hybrid.
 P_3 =great-grandparents, etc.

results; for instance, $Wn c \times Wn C$ and $Wn C \times Wn c$ both give $WWNnCc$. There are, however, twenty-seven different combinations amongst the sixty-four matings; these, together with the number of matings in which each occurs, are shown in Table II.

TABLE II.—*The twenty-seven different types in the second generation of a hybrid between a winter wheat, W, with weak straw, n (absence of nonlodging character), and open chaff, c (absence of closed chaff), and a spring wheat, w (absence of winter character), with stiff straw, N (nonlodging), and closed chaff, C.*

Serial No.	Proportions.	Formulae of the types.	Serial No.	Proportions.	Formulae of the types.	Serial No.	Proportions.	Formulae of the types.
1	1	$WWNNCC$	10	2	$WwNNCC$	19	1	$wwNNCC$
2	2	$WWNnCc$	11	4	$WwNnCc$	20	2	$wwNnCc$
3	1	$WWNNcc$	12	2	$WwNNcc$	21	1	$wwNNcc$
4	2	$WWNnCC$	13	4	$WwNnCC$	22	2	$wwNnCC$
5	4	$WWNnCc$	14	8	$WwNnCc$	23	4	$wwNnCc$
6	2	$WWNncc$	15	4	$WwNncc$	24	2	$wwNncc$
7	1	$WWnnCC$	16	2	$WwnnCC$	25	1	$wwnnCC$
8	2	$WWnnCc$	17	4	$WwnnCc$	26	2	$wwnnCc$
9	1	$WWnncc$	18	2	$Wwnncc$	27	1	$wwnncc$
	16			32			16	

16+32+16=64.

Types Nos. 1, 3, 7, 9, 19, 21, 25, and 27 are homozygote, and will all reproduce true to seed. Type No. 1 was the type sought in this cross.

The first nine of these twenty-seven types, constituting one-fourth of the whole generation, are pure winter wheat (WW), the next nine (Nos. 10–18), constituting one-half of the generation, are hybrids between winter and spring (Ww), while the last nine, constituting one-fourth, are pure spring wheats (ww). Each of these three groups of nine types is subdivided in like manner into one-fourth pure nonlodging, one-half hybrid between lodging and nonlodging, and one-fourth pure lodging. Thus, the first three types are all pure winter and pure nonlodging; these three types constitute 4 sixty-fourths of the generation, or one-fourth of the first group of nine. The second group of three are all pure winter, but hybrid with reference to the lodging character; these three constitute 8 sixty-fourths of the generation, or one-half of the first group of nine, etc. Thus, each of the three groups based on the winter-spring character pair is subdivided into three groups based on the straw character, thus giving nine groups based on these two character pairs. Each of these nine is similarly divided into three types, based on chaff character. This gives in all twenty-seven different combinations. Of these twenty-seven combinations, eight are seen to be homozygote with reference to all three character pairs. This means that these eight are pure bred as far as these characters are concerned and will show these characters in all their progeny. The other nineteen types are heterozygote, or cross-bred, with reference to one or more of the character pairs, and will thus not reproduce true to seed.

The one combination which was sought in this cross is type No. 1 of Table II. This type constituted only 1 sixty-fourth of the second generation of this hybrid. It is the combination *WWNNCC*, which is pure winter wheat, nonlodging, with tightly closed chaff. The most undesirable type, *wwnncc*, also occurred once in sixty-four times—that is, it was a spring wheat which lodged and had weak chaff. Further mention of this new type of wheat will be made later in discussing the application of the principles to plant breeding.

We may now state the law of recombination as follows: In the second generation of a hybrid there tends to occur every possible combination of the original parent characters.^a

We may further add to this law that every one of these combinations will, if the second generation is numerous enough, occur in some individuals in homozygote form, and will thus be firmly fixed and reproduce true to seed.

Although all the possible combinations will occur in the second generation of a hybrid (that is, provided the second generation is numerous enough to permit them to occur) unfortunately most of them will be mixed with other combinations that have the same external appearance but very different hereditary tendencies. This is due to the fact of dominance. For instance, the homozygote form *WWNNCC* of Table II can not be told by inspection from the form just following it (*WWNNCc*) or from several other of the twenty-seven combinations. One way to overcome this difficulty in a self-pollinated species is to save the seed of each second-generation plant separately. If the species is one that is not self-fertilized, but one which can be artificially self-fertilized, we can accomplish the segregation of the desired type by artificial self-fertilization of all the second-generation individuals that appear to be of the type desired and by planting their seed separately. When the next generation matures it will be seen which of them have reproduced true to type. The seed of these may be saved, and thus form the basis of a new and fixed variety in self-fertilized species and in such open-fertilized species as will endure such self-fertilization.

A very beautiful illustration of the law of recombination is seen in the work of Professors Price and Drinkard, of the Virginia Agricultural Experiment Station, in their experiments with hybrid tomatoes. Two varieties were crossed which differed in three respects, namely, one variety had green leaves, the other yellowish green; one had red fruit, the other yellow; one had pear-shaped fruit, the other round.

^a The writer discovered this law independently in 1901. See Bulletin No. 115, Office of Experiment Stations, U. S. Dept. of Agriculture.

In the second generation of this hybrid every one of the eight possible combinations of these three pairs of characters was found, as follows:

Serial No.	Leaf color.	Fruit color.	Fruit shape.
1.....	Green.....	Yellow.....	Round.
2.....	Green.....	Yellow.....	Pear-shaped.
3.....	Green.....	Red.....	Round.
4.....	Green.....	Red.....	Pear-shaped.
5.....	Yellowish.....	Yellow.....	Round.
6.....	Yellowish.....	Yellow.....	Pear-shaped.
7.....	Yellowish.....	Red.....	Round.
8.....	Yellowish.....	Red.....	Pear-shaped.

Two of these eight types were like the original parent varieties, the other six were new. This case illustrates well the power a knowledge of the law of recombination puts into the hand of the breeder. Breeders have unconsciously used this law since breeding first became an art, but a knowledge of the principles involved now enables them to accomplish desired results much more quickly and surely than was formerly the case.

FLUCTUATING VARIATIONS.

From what has been said concerning the law of recombination it is easy to see that in a species which naturally cross-fertilizes in the field we are continually getting new combinations of hereditary characters. For instance, in a cornfield hardly any two plants can be found that carry exactly the same combination of hereditary characters. If we should take a single grain of corn and plant it where it can not cross-fertilize with another its progeny would break up into types somewhat as shown in Table II, except that, instead of stopping with twenty-seven different types, each of these would be subdivided into three others, and each of these again subdivided in the same way, and so on within the limits of the number of separate and independent hereditary characters for which the grain we started with was heterozygote. Generally speaking, only a comparatively few of these characters will be important to the breeder, so that the others may be neglected. But we must not overlook the fact that in the main the remarkable fluctuations of characters seen in a cornfield are due to this recombination of characters from year to year. On the other hand, if we take a single grain of wheat and plant it, then save every seed of it for planting, the plants produced in the second generation would, ordinarily, be exactly alike in so far as their combinations of hereditary characters are concerned. This is because under ordinary field conditions wheat is self-fertilized, and a field of wheat in the main consists of plants that are completely homozygote with reference to every one of their hereditary characters. When we do get

a plant which is completely homozygote in all its characters, then it will transmit the same form of every character to all its offspring, and we have eliminated all variations due to recombination of characters. There will still be differences between the plants grown from the same seed, but these differences will be due to environmental influences, such as differences in available moisture, plant food, sunlight, and the like. It is highly important to make this distinction between individual variations which are due wholly to environment and those which are due to recombinations of hereditary characters. It will be seen later that so far as experimental evidence goes there is much reason to believe that selection of those fluctuations which are due wholly to environment as a rule has no effect whatever in changing the hereditary characters of the plant. On the other hand, in those plants which are not homozygote in all their characters, as is practically always the case in a species that regularly cross-fertilizes, there will be variations due to recombinations of different characters, and selection will have a marked effect in species of this kind. The effect of selection on fluctuating variations has been much confused because of the effect produced by mass selection in mixed populations of fixed forms like wheat, which effect will be further discussed later. In wheat, and other self-fertilized species, individual selection—that is, selection in which we keep the progeny of each mother plant separate—soon proves that we can not modify these fixed strains by selection; that is, generally speaking. The facts have further been confused because of the effect which either mass or individual selection has in gradually changing the character of cross-fertilized crops like corn. In these cross-fertilized crops either mass selection or selection annually to a single mother plant causes a gradual change in the direction of the selection. But when we eliminate the effect of the law of recombination, which occurs continually in cross-fertilized forms, and practice selection annually to a single mother plant, we find that it is apparently impossible to produce modification by selection, except in rare instances. The investigations on which this reasoning is based will be given later in these pages.

The amount of investigation which this subject has received can hardly be said to be sufficient to settle it for all cases, for there are a few exceptional cases which do not behave in the usual way and which are not understood. In the main, however, the investigations all agree. The first work bearing strictly on the effect of selection on forms from which all variation other than fluctuating variation due to environment has been eliminated was done by Prof. W. Johannsen, of Copenhagen, on beans and barley. This work will be referred to more in detail when we come to consider the effect of selection on self-fertilized species, as will also the remarkably accu-

rate work of Doctor Nilsson, whose work at Svalöf, Sweden, is so well known through the writings of De Vries. Some of the work on vegetatively propagated species will be given in dealing with the effect of selection on this class of plants.

RUNNING OUT OF VARIETIES.

It is quite generally believed that there is a tendency for vegetatively propagated varieties to "run out." This subject has received much discussion but very little careful investigation. There is no question that in many species such varieties do lose vigor and become practically worthless after a few years. Carnation growers all agree that varieties of these plants are short lived. Varieties of carnations seldom retain their vigor a dozen years. It is generally believed that varieties of potatoes retain full vigor only for a few decades. With no selection this is undoubtedly true. We do not know just what effect careful selection to maintain yield might have on the length of life of a variety of potatoes. It is certain, however, that the old Peachblow potato, so popular half a century ago, has been maintained in full vigor by selection to the present time. Mr. E. H. Grubb, of Colorado, one of the leading potato growers of that State, is now growing this variety and finds it an excellent yielder. It is probable, however, that potato varieties do tend to run out. The same may be said of apples, but, as in the case of potatoes, definite investigations on this point are lacking.

On the other hand, there are species that have completely lost the power of producing seed, as, for example, the banana. These have been propagated vegetatively for ages without loss of vigor. But we can not say that the same variety persists indefinitely, because the facts are wanting. It is probable that among vegetatively propagated races we may find every gradation between races which run out very quickly and those which remain vigorous indefinitely.

A good many species of plants produce seeds parthenogenetically,^a as the dandelion, certain species of Hieraceum, etc. These are among our most vigorous weeds. How long they have propagated asexually we do not know. They may, however, be cited as instances of plants which apparently retain their vigor through long periods without recourse to sexual propagation.

What has been said of races propagated vegetatively applies equally to those which are habitually self-fertilized, with perhaps the difference that in most such species there may occasionally occur cases of cross-fertilization. It is quite generally assumed that self-fertilized races tend to run out. There is some evidence that

^a That is, without fertilization. In these plants the reduction division is omitted in those mother cells which develop into seeds.

such is the case. This is especially true of varieties of wheat. A single variety seldom retains its supremacy in any given locality for half a century. Yet it is far from demonstrated that careful selection of wheat varieties would not maintain vigor almost indefinitely. This whole question of the running out of varieties needs much further study before the last word can be said on the subject.

Having outlined the main principles with which we have to deal in plant breeding, we may now proceed to a consideration of the different methods of breeding and selection and the application of the principles involved.

SELECTION WITHOUT ARTIFICIAL CROSSING.

We have already seen that close-fertilized and cross-fertilized species behave differently under selection. In addition to self-fertilized and cross-fertilized species we must also consider the effect of selection on those varieties which are propagated vegetatively; that is, from cuttings, grafts, tubers, etc., including all methods of propagation other than from seed.

VEGETATIVE PROPAGATION.

In plants propagated vegetatively we have several kinds of variation to consider, for the effect of selection on each of these is different. First, we have those fluctuating variations which are due wholly to environment, such as difference of food supply, moisture conditions, etc., which modify the individuals of a generation but which are not hereditary. As we have already seen, such investigations as have been made on this subject indicate that in nearly all cases of fluctuating variation due to environment selection is entirely without permanent effect in changing the plant from year to year. In Bulletin No. 127 of the Illinois Agricultural Experiment Station Dr. E. M. East made a careful survey of all the literature he could find relating to the effect of selection on these fluctuating variations in potatoes. He concluded that it is not proved that selection can change these variations, though the question is left in some doubt.

Prof. H. S. Jennings, of Johns Hopkins University, has during the past few years made some investigations on the unicellular animal *Paramecium* which must rank among the most important biological work that has been done, at least in the field of experimental evolution. While *Paramecium* is an animal, it propagates for hundreds of generations by simple division, and hence there is every reason to suppose that the principles applicable to *Paramecium* are applicable to plants which are propagated vegetatively. Jennings gives an excellent summary of his work in the *American Naturalist* for June, 1909, where reference will be found to the original technical

publications. First, he studied abnormal individuals to see whether or not their abnormalities were inherited. In many of his cultures, individuals could be found that had various peculiarities. Although he sought patiently for some peculiarity of this kind that might be inherited and although he found many such peculiarities, in no case did he find one that is inherited in the proper sense of the word. The peculiarities in question never appeared in both of the individuals resulting from a division. Thus there was no tendency for them to multiply and spread over the race. Concluding his discussion of such cases, Jennings remarks: "Examination of a large number of cases in *Paramecium* shows that these untypical characters are never reproduced in the young."

Jennings also found that the descendants of a single individual varied greatly in size. This suggested the idea that by selecting continually from the largest and the smallest, two races could be developed which would differ in size, although descended from the same original individual. This experiment was carried on for a very long series of generations, one line consisting of the largest individuals that could be found and of their largest progeny, the other of the smallest individuals and their smallest progeny. At the end of the experiment the two lines were brought under the same environmental conditions and within a very short time the average length of the two types became identical. This led Professor Jennings to remark that "Selection within a pure race is of no effect on size," and again, "Neither selection nor environmental action changes the size of the pure race."

This investigator found eight distinct types of *Paramecium* in a group which was previously supposed to consist of two species differing in size. Figure 1 illustrates the relative sizes of the individuals in these eight races. It is seen that even the extreme forms overlap, and it was found that if the smallest individual of the largest race be selected and its progeny grown with continual selection from the smallest individuals to be found, no matter how long such selection was continued the progeny of this small individual would soon cover the whole gamut of variation of the race to which it belonged, and the same was true for each of the other races. Speaking of the effect of selection on such a species, Jennings says:

How will selection act on such a complex species? As we have seen, selection within a single race is without effect. But if we make selections among the individuals of a mixed collection of races, such as figure 1 shows, we reach most instructive results. By making our selections in the proper way, we for a time make steady progress toward a certain goal. We will suppose that we do not know of the existence of these races; this is the case with most experiments in selection. From the species as a whole, as shown in figure 1, we will select for increased size. Let us follow the old plan of selecting many individuals showing the desired character; we will preserve all specimens above the mean size of the entire collection; that is, we divide the

collection at $x-x$, rejecting all those to the right. By so doing it is evident that we exclude all specimens of the two smallest races c and i , while preserving the majority of the specimens of the larger races. Allowing these to propagate, we of course get a mixture of the remaining larger races. Hence the mean size of the whole collection will be greater than at first. Selecting again those above the mean size of this lot, we drop out another small race, and the mean of the collection as a whole again rises a little. We are making good progress in the improvement of our species. By taking successive steps of this character, dropping out the smaller races, first partly, then completely, one after another, we can for a long time continue to improve by

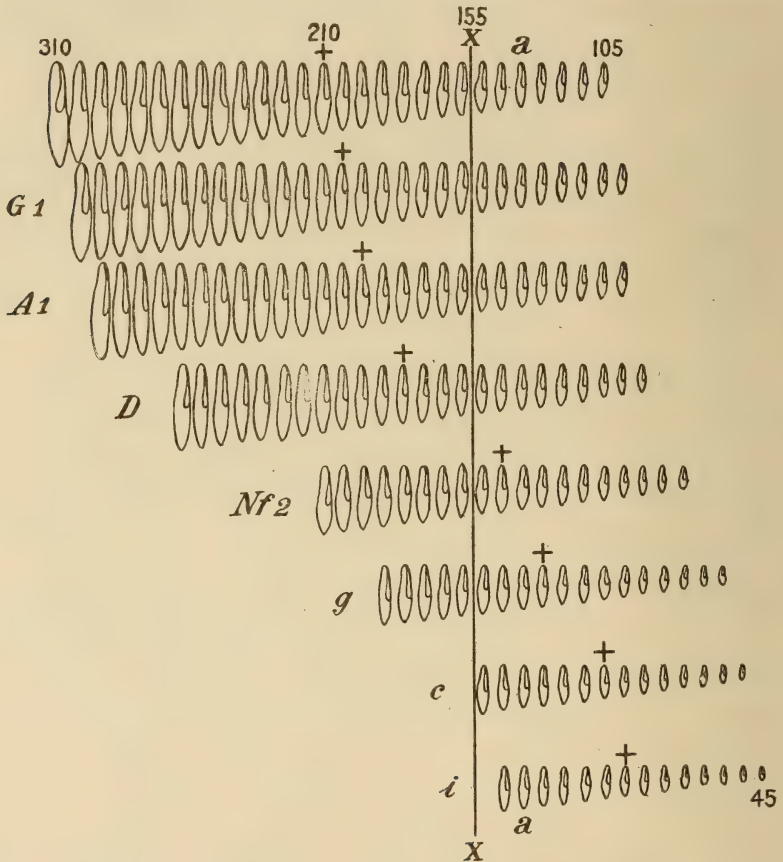


FIG. 1.—Graphic illustration of the range of fluctuations of each of the eight pure races of *Paramecium* studied by Jennings. (Reproduced from the *American Naturalist*.)

selection, but finally we reach a stage in which all but the largest race have been excluded. Thereafter we can make no further progress. In vain we choose for breeding the largest specimens of the lot; all belong to the same race, so that all produce the same progeny. Selection has come to the end of its action. * * *

Selection here consists simply in isolating already existing races. It produces nothing new. * * *

Systematic and continued selection is without effect in a pure race, and in a mixture of races its effect consists in isolating the existing races, not in producing anything new.

Similar work with identically the same result has been done on hydra by Elise Hanel^a and by M. A. Barber^a on yeasts and bacteria. In Barber's work there were some exceptional cases which will be mentioned later. He found many races of each, but each race was constant, with the exceptions noted below. Long-continued selection had no effect in changing one of these races. Barber also studied individuals having various peculiarities. While the vast majority of these peculiarities behaved exactly as Jennings found them to do in *Paramecium*, he did find a few cases within a pure race (that is, in the descendants of a single individual) that transmitted their peculiarities to their descendants. Here we have actual evolutionary change in a race. Races of yeast were produced having cells of different form from the parent type and races of bacteria composed of longer rods than the parents, but such cases were extremely rare. Thus we must assume that there are occasionally permanent evolutionary changes. As to the amount of change in such cases we can get some information from Jennings's races of *Paramecium*, assuming, of course, that the differences between the various races have come about by evolutionary change. The difference between the average size of the two smallest races of *Paramecium* studied by Jennings was only 0.00028 inch, yet the progeny of any individual, large or small, in either of these two races, accurately maintained this difference between the races. The important point in all this is that when we are dealing with individuals of a pure race, or, as Webber calls them, a "clonal" race of variety—that is, individuals descended from a single individual by vegetative propagation—except for those very rare cases in which positive evolutionary change occurs the fluctuating differences between individuals have absolutely no bearing on the evolutionary process. According to Jennings there seems little doubt that this is true for organisms in general. He says:

In *Paramecium*, in the extensive study of many races for hundreds of generations by exact statistical and experimental methods, not one single instance was observed of variation in the sense of an actual change in the race.

So far as the evidence goes every race is essentially the same throughout the work and may have been the same for unnumbered ages.

Jennings emphasizes the fact that real evolutionary changes do not occur often or easily. "The fundamental constitution of the race is resistant to all sorts of influences. It changes only in excessively rare instances and for unknown causes."

In summarizing his conclusions, Jennings makes the following statement: "Until some one can show that selection is effective within pure lines it is only a statement of fact to say that all the experimental evidence we have is against this."

^a Cited by Jennings in *American Naturalist*, June, 1909.

The following statement is made by Dr. Raymond Pearl and Mr. Frank M. Surface in Bulletin No. 166 of the Maine Agricultural Experiment Station:

There is a rapidly accumulating mass of evidence that the chief, if not the entire, function of selection in breeding is to isolate pure strains from a mixed population. It is found in actual experience impossible to bring about by selection improvement beyond the point already existing in the pure (isolated) strain at the beginning.

These writers do not here distinguish between the effect of selection in self-fertilized and cross-fertilized species, but what is said does apply to close-fertilized species strictly, where hybridizing is not practiced, and with certain limitations it also applies to cross-fertilized species, as will be seen later.

If the conclusion that selection of fluctuating variations is without effect is correct, then it follows that after we have by trial found the best individuals in a crop propagated vegetatively we have gone as far as selection enables us to go, except as immediately stated below.

But there is a second type of variation in vegetatively propagated crops which can be affected by selection. Each individual plant is endowed with a certain number of hereditary characters. These characters may or may not come to complete development under given environmental conditions, or some of them may reach complete development while others may fail to do so. In so far as this failure to develop is due solely to environmental conditions selection is without power to modify the crop. But it would appear that from time to time, or perhaps more or less continuously, changes are going on with reference to these hereditary characters by which their tendency to develop under given conditions changes; so that in a crop like potatoes we may in time get a good many varieties from the descendants of a single individual. But these varieties, in the main, arise by certain hereditary characters becoming latent or possibly in some cases disappearing altogether. Again, it may be that the tuber with which we start a race may have a good many latent characters in it whose tendency to develop may subsequently increase, so that occasionally we get a variety which differs from that with which we started by the development of certain characters which were not patent in our original stock. For instance, a white variety may produce tubers with colored skin. Color is especially likely in white varieties to occur in the vicinity of the eyes of the tuber.

The more usual variation which occurs in such cases is for characters that are present to become latent, so that we are more likely to get light color or white from colored stock.

What has been said about variation in vegetatively propagated plants applies also to bud variations, or the so-called "bud sports."

In nearly all cases these sports differ from the plant on which they originated by lack of characters that are visible in the mother plant. Occasionally, however, the reverse is true. But when a new character appears in a bud sport it is in nearly all cases a character common to the species, which was presumably latent in the mother plant.

The Ethel Maule dahlia furnishes what appears to be an example. This is sold as pure white. Mr. W. A. Andrews, of Washington, D. C., has grown this dahlia for four years. Last year (1908) one of the plants produced flowers having a decided pink tinge, especially in the center of the flowers. This year he has several of the plants produced (by division) from the pink-flowered one of last year, and all of them show the pink color. All the plants of this variety in Mr. Andrews's garden have been propagated by division from a single plant obtained four years ago. Presumably the pink color is latent in the original stock and has been partially revived in these pink-flowered individuals.

In those vegetatively propagated plants where variation occurs by hereditary characters becoming latent—and this type of variation seems to be quite common, especially in potatoes—selection of seed is of great importance. In this case selection enables the breeder to keep his stock up to standard, at least much longer than would be the case without selection, and where variation occurs by the development of characters which were previously latent it enables him to preserve such variations when they are of value.

The results of the application of the principles here stated to the selection of seed potatoes have been in some cases quite marked. For instance, a potato grower in Michigan some years ago began the practice of digging by hand enough potatoes for seed and saving only those hills that had six or more merchantable tubers and no small tubers. When he first began this practice he found only sixteen hills out of each hundred dug that came up to his standard, but after he had continued the practice for five years the number of such hills had risen to seventy in a hundred. Under the direction of Mr. L. G. Dodge, of the Office of Farm Management, several New England potato growers have been applying these principles for two years past. The first year there was an average of about eight hills per hundred that came up to standard. The second year from seventeen to twenty hills met the conditions. This is as far as the experiment has proceeded at the present time. Some work done on potatoes by Mr. C. W. Waid, of the Ohio Agricultural Experiment Station, has given similar results. In this work, starting with the same original lot of tubers, three strains were grown, as follows: (1) Seed from high-yielding hills, (2) seed from low-yielding hills, and (3) unselected

seed. Taking the yield of the unselected seed as a basis, the results were as follows:

Source of seed.	1904.	1905.	1906.	1907. ^a	1908. ^b
From high-yielding hills.....	122	127	147	125	171
From unselected hills.....	100	100	100	100	100
From low-yielding hills.....	70	55	77	66	91

^a See Report, American Breeders' Association, vol. 3, p. 191 et seq.

^b See Circular No. 90, Ohio Agricultural Experiment Station.

SELF-FERTILIZED SPECIES.

The effect of selection on self-fertilized species, such as wheat, barley, and oats, is essentially the same as it is on species propagated vegetatively. Doctor Nilsson in his remarkable work at Svalöf, Sweden, has many times taken an unselected lot of seed from some cultivated variety of wheat or oats and planted each seed individually to study the character of the plants produced. He rarely finds two plants exactly alike. But when he saves the seeds from these plants separately the next year the progeny of each plant is, as a rule, found to be so much like the parent plant as to be indistinguishable from it except for such fluctuations as may be due to environmental influences only.

Occasionally in work of this kind a plant is found which is not homozygote in all its characters. In other words, it is not absolutely pure bred. These plants split up in the next generation according to the law of recombination. Furthermore, their presence indicates that there is occasionally cross-fertilization in wheat and oats, so that ultimately in a wheat field there may be found practically every possible combination of all the characters present in the field, and in time every one of these combinations will come to exist in some individuals in homozygote form; for, as will be seen later, a self-fertilized plant tends to split up into all the fixed forms which can be made from the various combinations of the characters present in it.

Neglecting for the present the occasional cross-fertilizations in a field of wheat or oats and the resulting heterozygote plants that are produced in this manner, which will be considered under the next heading, selection without cross-fertilization in self-fertilized species can have no effect except to enable the breeder to find those individuals which are best among the population with which he is dealing. After he has found these individuals he can not improve them by selection. On the other hand, he may be able to hold them up to a high standard by means of selection, for presumably, as in the case of potatoes, the hereditary characters present in wheat may change in their tendency to develop. Especially may characters that are present get into the habit of failing to develop and thus

give rise to inferior plants in the progeny of what was originally a high-class individual.

While experimental evidence for the above statements is not as plentiful as it ought to be, Doctor Nilsson has done so much work along this line that the propositions enunciated may be considered practically established. Professor Johannsen, of Copenhagen, has done a great deal of work of the same kind with exactly the same results. At the 1906 Genetic Conference in London he said, "In a population containing only one single type the selection of fluctuations has no action at all." Johannsen has several races of beans which he has grown pure for several years and which are fully homozygote. He has fully tested the effect of selection on certain seed characters of these beans. Speaking of the results,^a he says, "Selection for weight, for absolute length, or relative breadth has had absolutely no observable influence on these characters." Johannsen has obtained similar results with barley.

After what we have seen to be true in vegetatively propagated races it should not be surprising that similar results occur in self-fertilized races, for although such races go through the form of recombining the characters when they produce seed, the two members of each pair of characters being exactly alike, we get no new combinations, so that reproduction by seed in completely homozygous strains differs little, if at all, in its results from vegetative propagation.

The fact that in a field of a self-fertilized crop a very large majority of the plants are perfectly fixed in their hereditary characters and will reproduce themselves with almost absolute fidelity from seed has led a good many biologists to consider every one of these plants which differs from its neighbors in any way to be what they call "elementary species." They overlook the fact that these forms are fixed simply because they are homozygote in all their characters and would behave in exactly the same manner whether the evolutionary changes that produced them are either very slow and gradual or occur suddenly at long intervals.

The problem, then, in selecting self-fertilized plants is to find the best individuals and propagate from them. There are two ways of selecting such plants, which give somewhat different results. One of these we may term "mass selection," the other "individual selection."

MASS SELECTION.

Mass selection is that form of selection in which a number of superior plants or parts of plants are chosen but their seed is not kept

^a *Zeitschrift für Induktive Abstammungs- und Vererbungslehre.* September, 1908, p. 2.

separate. It may happen that some of the selections thus made are superior because they have been grown under very favorable environment and that another year when the environment is less favorable they may prove to be very inferior. Others may prove to be superior under a wider range of environmental conditions, so that from year to year they will be superior. The next year mass selection would be mostly from those plants which are what we may call permanently superior, together with a few of those which merely happen to be superior under the given conditions. The continuation of mass selection thus tends to improve from year to year the general character of the crop, but it does this by the gradual elimination of the progeny of those plants which are not superior except under very favorable conditions. This gradual improvement that occurs in mass selection has misled biologists and plant breeders generally into believing that selection could affect fluctuating variation.

The effect of mass selection of self-fertilized crops is well illustrated by some of Prof. C. A. Zavitz's work at Guelph, Ontario, Canada. In his annual report for 1905 he gives the results of sixteen years' continuous mass selection on oats and barley. These are given below. For convenience, his results obtained by similar methods with potatoes are also given here. It will be noticed that mass selection has the same effect in self-fertilized wheat and oats as in potatoes, which are propagated vegetatively.

TABLE III.—Average yields by four-year periods, in bushels per acre, of oats, barley, and potatoes, showing the effect of mass selection on self-fertilized and on vegetatively propagated crops.

Crops.	1890-1893.	1894-1897.	1898-1901.	1902-1905.
	<i>Bushels.</i>	<i>Bushels.</i>	<i>Bushels.</i>	<i>Bushels.</i>
Oats, average for 8 varieties.....	74	79	83	100
Barley, average for 8 varieties.....	50	54	63	63
Potatoes, average for 7 varieties.....	120	216	218	249

The very marked effect in the case of potatoes is probably due to degeneration which had occurred in many vegetative strains before the selection began, the progeny of these degenerate strains being gradually eliminated by mass selection.

The Mandscheuri barley, now so largely grown in Ontario, is descended from a single pound of seed obtained from Prussia in 1889. Of this variety 567,000 acres were grown in Ontario in 1908. Since the introduction of Mandscheuri, the barley crop of Ontario has increased in value from \$4,800,000 to \$12,900,000, and this is in part due to the larger yielding power of this variety. The greater profit due to larger yields has caused an increase in acreage.

INDIVIDUAL SELECTION.

In the form known as individual selection we start with superior plants and keep their seeds separate. This enables us very quickly to determine which of the original selections are superior under a wide range of conditions, so that within a few years we can determine which of our original selections represent the best strains in the variety. Then by propagating from them and by continuously selecting to avoid saving any plants which may be deteriorating from hereditary characters becoming latent, we can maintain the variety at a high standard. But it must be remembered that we can not increase the superiority of a pure strain by selection except in those comparatively rare cases where characters that were latent in our original selection change in their tendency to develop and happen to increase the superiority of the strain.

That latent characters may reappear in a variety is shown by the following facts. Sometimes, in varieties of potatoes having white skin, tubers are found which have purplish or red skin, at least over part of the surface, and especially about the eyes. Bud sports sometimes exhibit characters not apparent in the parent stock, but common to other varieties of the species. In Doctor Nilsson's work at Svalöf, Sweden, black or yellow oats occur at wide intervals in white varieties. All these facts indicate that latent characters occasionally become patent.

We have already referred to the effect of mass selection on barley at the Ontario Agricultural Experiment Station. Professor Zavitz has also used individual selection on varieties of this crop. In 1903 he selected 9,972 grains of the Mandscheuri barley and planted them individually. Seed of 33 of these were planted separately in 1904. By 1908 all but three of these strains had been discarded. One of these, known as "O.A.C. No. 21," which outyields the original variety, is now rapidly replacing the latter on Ontario farms.

The selection at the Minnesota station, begun by Prof. Willet M. Hays, is individual selection. The seed of each plant, to serve as the original parent of a strain, is saved separately, so that the yielding power of pure strains is determined by several years' test of successive generations of their self-pollinating progeny. The best of these are finally brought into culture. This method enables the breeder to secure the best strains present in the seed with which he starts, or, as Professor Hays puts it, it enables the breeder to find those plants having the highest "centgener" power; that is, the power of producing strains with maximum yields under the widest range of environmental conditions. Some of the wheats obtained in this manner at the Minnesota station have proved decidedly superior to the original mixed stock from which they were isolated.

In these homozygote forms, which constitute the major part of a field of any crop which habitually self-fertilizes, there is little, if any, more variation than in plants which are propagated vegetatively.

CROSS-FERTILIZED SPECIES.

The effect of individual selection on cross-fertilized species, such as corn, is very different from what it is in self-fertilized species. Here the plants chosen are more or less cross-fertilized with other plants and the seeds obtained from a single plant are not all alike in content of hereditary characters. Hence we may get distinct differences in the individuals grown from this seed. Either mass selection or individual selection in a crop of this character may make decided changes in it for the reason that, in the seed of every plant, combinations of hereditary characters will occur that are unlike those in the original plants selected. Some of these may be superior to the original plants. For instance, the plant with which we start may be heterozygote with reference to a particular character which we will call "A." That is, it inherited from one of its parents the presence of this character and from the other its absence. Its formula with reference to this character would therefore be Aa . Such a plant will produce progeny one-fourth of which has the formula AA , one-half Aa , and one-fourth aa . Now, the combination AA may be superior to Aa and aa , so that in the seed of our selection we may get something better than the plant selected. On the other hand, we may also get something not so good. Selection alone, therefore, enables us to make positive improvements in crops which regularly cross-fertilize.

The work done on the corn plant at the Illinois Agricultural Experiment Station is perhaps the best illustration of the effect of selection on crops that cross-fertilize. Bulletin 128 of that station gives the results of ten years' selection of corn for high and low oil content and for high and low protein content. Some of these results are given in Table IV.

TABLE IV.—*Effect of selection in a cross-fertilized species. The figures of column 2 give differences in percentage content of oil between two strains of corn of similar origin, one selected for high and one for low oil content. Column 3 gives similar differences between two other strains selected, one for high and the other for low protein content.*

Years.	Oil differences.	Protein differences.
	<i>Per cent.</i>	<i>Per cent.</i>
1896	0.00	0.00
1897	.67	.55
1898	1.16	.50
1899	1.82	1.60
1900	2.55	2.98
1901	2.66	4.08
1902	3.39	4.12
1903	3.53	4.52
1904	4.08	5.76
1905	4.71	6.15
1906	4.71	5.62

Bulletin 132 of the same station gives the results of six years' selection of corn for high and low ears. See Table V.

TABLE V.—*Difference between two strains of corn selected for ears high or low on stalk.*

Years.	Difference in height of ears.	Difference in number of inter- nodes in stalks.
	<i>Inches.</i>	<i>Number.</i>
1903	13.6	1.5
1904	12.0	1.5
1905	21.7	1.8
1906	31.1	4.1
1907	39.2	3.3
1908	34.2	4.0

Another instance of the effect produced on a species which is partially cross-fertilized is seen in some interesting work of Professor von Rümker at the Breslau Experiment Station in Germany. This work was done on rye, in which species more or less cross-fertilization occurs. By continued individual selection for color of seed Professor von Rümker finally obtained several strains of markedly different color. Yellow color was more difficult to fix than green. This is probably due to the compound nature of the yellow color from the Mendelian standpoint. Some interesting cases of correlation were found in this work. Green-colored seeds produced stronger stalks; brown seeds were less winter hardy. It was found that the selection must be continued in order to maintain the characters for which the selections were made. It is doubtful if these results could have been obtained in a strictly self-fertilized species.

The reason why selection produces these effects on cross-fertilized plants is seen in the following: Suppose we start with a corn plant that is heterozygote for yellow and white corn and for starchy and sweet corn characters. The presence of yellow may be represented by Y , the absence of yellow (that is, white) by y ; the presence of starch-forming character by S , and its absence (that is, sweet-corn character) by s . Figure 2 shows the nine different types of corn which would be produced by the individuals. If, now, we plant all the seed produced by these nine types of corn and plant them where they can freely cross-fertilize, but where they will not cross with other kinds of corn, the next year we shall again get these same nine types, but not in exactly the same proportion. If corn were completely cross-fertilized the proportion of these nine types would be approximately the same the second year, and each year thereafter, assuming, of course, that all the types are equally productive. This is illustrated in figure 2. On the other hand, if corn were completely self-fertilized, these nine types would behave as those shown in fig-

ure 4, where four of the nine types increase and five decrease until, in ten generations, the whole population consists of little more than an equal mixture of the four homozygote types. Corn, being largely but not completely cross-fertilized, would give a result intermediate between those shown in figures 2 and 4. If the amount of cross-fertilization in corn were fixed and definite, and if the average percentage of cross-fertilization could be determined, it would then be possible to calculate the exact percentage of each type present in the

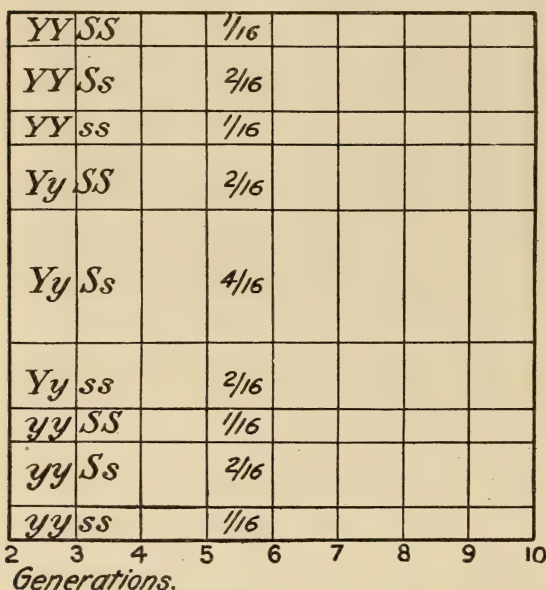


FIG. 2.—Graphic illustration of ten generations of corn with no selection, the first generation of which is $YySs$.^a The proportion of each type is indicated by the vertical space between the horizontal lines above and below the type symbols. Thus, $YYSS$ is one-sixteenth of the whole population. Under the conditions mentioned each type tends to remain in the same proportion from year to year.

eration to generation. This means that each of the nine types present tends to remain in the same proportion from generation to generation under these conditions.

One method of arriving at the data shown in figures 2, 3, 4, and 5 is illustrated immediately below, for those cases in which there is complete cross-fertilization, as in animals and in dioecious plants. Generation F_2 in hybrids whose parents differ in one Mendelian character only is $1DD$, $2DR$, $1RR$, where D represents the dominant and R the recessive character. Hence one-fourth of generation F_2 consists of the type DD , two-fourths of type DR , and one-fourth of type RR . But since males and females are equally numerous, one-fourth

the population after the relation between the types became constant; also the rate at which each type approached its ultimate proportion of the population.

Figure 2 shows what would happen if corn were completely cross-fertilized. This figure will be understood when it is explained that the space between any two adjacent horizontal lines represents the proportion of the population of the type represented by the formula in that space. Here each of the nine spaces maintains the same width from generation

^a Complete cross-fertilization is here assumed. The actual results are intermediate between those shown in figures 2 and 4.

of the males are of type *DD*, two-fourths of type *DR*, etc., and similarly for the females. Now a female of type *DD* may be fertilized by a male of any of the three types, and the probability that a given female shall be fertilized by a male of a particular type will depend on the relative number of males of that type. Since one-fourth of the males are of type *DD*, the chance that any particular female shall be fertilized by a male of type *DD* is one-fourth. Since one-fourth of the females are of type *DD*, the chance that in a particular mating the female shall be of type *DD* is one-fourth. Hence the probability that a given mating shall be of type *DD* ♀ × *DD* ♂ is $\frac{1}{4} \times \frac{1}{4} = \frac{1}{16}$. The possible matings that can occur, and the relative probability of each of these matings, is shown in the left-hand column of Table A. Since the denominator is the same for all these matings, it is omitted for convenience. The products at the right of column 1 represent the relative frequency of each of the matings. Assuming all these matings to be equally productive, these same numbers represent the relative number of progeny from matings of each of the types of matings.

TABLE A.—*Method of determining the relative proportion of the various types in the progeny produced by the individuals of generation F₂, with cross-fertilization.*

Matings and their relative frequency.	Types of progeny and their relative frequency from each of the possible matings.		
	<i>DD</i>	<i>DR</i>	<i>RR</i>
♀ <i>DD</i> × ♂ <i>DD</i> ...1 × 1 = 1.....	1		
<i>DD</i> × <i>DR</i> ...1 × 2 = 2.....	1	1	
<i>DD</i> × <i>RR</i> ...1 × 1 = 1.....		1	
<i>DR</i> × <i>DD</i> ...2 × 1 = 2.....	1	1	
<i>DR</i> × <i>DR</i> ...2 × 2 = 4.....	1	2	1
<i>DR</i> × <i>RR</i> ...2 × 1 = 2.....		1	1
<i>RR</i> × <i>DD</i> ...1 × 1 = 1.....		1	
<i>RR</i> × <i>DR</i> ...1 × 2 = 2.....		1	1
<i>RR</i> × <i>RR</i> ...1 × 1 = 1.....			1
Relative proportion in F ₃	4	8	4
Or.....	1	2	1

In the next three columns the relative proportions of the different types of progeny in each of the matings are shown. By adding these columns it is seen that the ratio between the types in F₃ is the same as it was in F₂. Hence it will tend to be the same in all subsequent generations, with cross-fertilization. With self-fertilization the results are different, as seen in Table B.

TABLE B.—Method of determining the relative proportion of the various types of progeny produced by generations F_2 and F_3 of a hybrid, with self-fertilization.

Types and their relative frequency.	Types of progeny produced by each F_2 type, and their relative frequency.		
	DD	DR	RR
Types in F_2 :			
1 DD ... a 2.....	2		
2 DR ... 4.....	1	2	
1 RR ... 2.....			1
Frequency of types in F_3	3	2	3
Types in F_3 :			
3 DD ... a 6.....	6		
2 DR ... 4.....	1	2	
3 RR ... 6.....			1
Frequency of types in F_4	7	2	7

a These numbers are taken instead of 1, 2, 1 (3, 2, 3 in F_3) to avoid fractions in the next three columns.

Here we see that the proportion of the types changes from generation to generation, the homozygote types increasing while the heterozygotes decrease in relative frequency.

It will be noticed that the sum of the relative frequencies in F_2 is 4; in F_3 , 8; and in F_4 , 16; and so on; that is, in F_2 it is 2^2 ; in F_3 , 2^3 ; in F_4 , 2^4 ; etc. In general, in F_n it is 2^n . Similarly, the frequency of each of the types DD and RR is, in

	F_2	F_3	F_4	F_5	F_6 -----	F_n
	1	3	7	15	31	

Or,

$2^1 - 1$	$2^2 - 1$	$2^3 - 1$	$2^4 - 1$	$2^5 - 1$	$2^{n-1} - 1$.
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The frequencies of all the types in F_n are—

$$DD, 2^{n-1} - 1$$

$$DR, 2$$

$$RR, 2^{n-1} - 1$$

$$2 \times 2^{n-1} = 2^n.$$

The above calculations have been made for a single character pair for convenience. Exactly the same method may be pursued when two or more Mendelian pairs are concerned, except that where two pairs are involved we must deal with nine types instead of three, and where three pairs are involved we must deal with twenty-seven types, and so on. In general, the number of types appearing in F_2 and later generations is 3^n , where the n is the number of character pairs involved.

To illustrate the effect of selection to a dominant type, let us consider the case of two character pairs, which we may denominate Aa and Bb , where A and B are dominant and a and b recessive. Generation F_1 produces nine types of progeny, which, with their relative frequencies, are shown in Table C. Here the selected types are those that have the appearance of the type $AABB$, namely, $AABB$, $AABb$, $AaBB$, and $AaBb$. It is seen that while type $AABB$ is only one-sixteenth of generation F_2 , it constitutes one-fourth of the selection made in F_3 . By continuing Table C to ten generations, the data from which figure 3 was constructed may be obtained.

TABLE C.—*Method of determining relative frequency of the various types in the progeny of generation F₂, with cross-fertilization, and selection to the dominant type, when two pairs of characters are involved.*

Matings.	Relative frequency of each type in the progeny of the various matings.								
	<i>AABB</i>	<i>AABb</i>	<i>AAbb</i>	<i>AaBB</i>	<i>AaBb</i>	<i>Aabb</i>	<i>aaBB</i>	<i>aaBb</i>	<i>aabb</i>
F ₁ , <i>AaBb</i> × <i>AaBb</i> 1×1=1....16 _a	1	2	1	2	4	2	1	2	1
F ₂ , <i>AABB</i> × <i>AABB</i> 1×1= 1....	1								
<i>AABB</i> × <i>AABb</i> 1×2= 2....	1	1							
<i>AABB</i> × <i>AaBB</i> 1×2= 2....	1			1					
<i>AABB</i> × <i>Aabb</i> 1×4= 4....	1	1		1	1				
<i>AABb</i> × <i>AABB</i> 2×1= 2....	1	1							
<i>AABb</i> × <i>AABb</i> 2×2= 4....	1	2	1						
<i>AABb</i> × <i>AaBB</i> 2×2= 4....	1	1		1	1				
<i>AABb</i> × <i>AaBb</i> 2×4= 8....	1	2	1	1	2	1			
<i>AaBB</i> × <i>AABB</i> 2×1= 2....	1			1					
<i>AaBB</i> × <i>AABb</i> 2×2= 4....	1	1		1	1				
<i>AaBB</i> × <i>AaBB</i> 2×2= 4....	1			2			1		
<i>AaBB</i> × <i>AaBb</i> 2×4= 8....	1	1		2	2		1	1	
<i>AaBb</i> × <i>AABB</i> 4×1= 4....	1	1		1	1				
<i>AaBb</i> × <i>AABb</i> 4×2= 8....	1	2	1	1	2	1			
<i>AaBb</i> × <i>AaBB</i> 4×2= 8....	1	1		2	2		1	1	
<i>AaBb</i> × <i>AaBb</i> 4×4= 16....	1	2	1	2	4	2	1	2	1
Frequency of types in F ₃	16	16	4	16	16	4	4	4	1
Relative frequency of selected types in F ₃	1	1		1	1				

^a 16 progeny assumed to avoid fractions in the table.

Since we do not know what percentage of cross-fertilization occurs in corn or any other open-fertilized crop, it has been assumed in what follows that corn is completely cross-fertilized. The actual results in practice would be intermediate between figures 2 and 4 when there is no selection to type and between figures 3 and 5 when there is such selection.

Referring again to figure 2, and supposing that we desire to select from this mixed population and perpetuate the type *YYSS*—that is, pure yellow starch-forming corn—we would at once discard the following forms: *YYss*, *Yyss*, *yySS*, *yySs*, and *yyss*. All of these would either be white or of the sweet type, or both. Discarding all these types that are not yellow starch-forming types, we would still have left the second, fourth, and fifth types shown in figure 2, all of which would be yellow and would have starchy grains, because the presence of these two characters is dominant over their absence, and these types heterozygote for one or both of these characters can not be distinguished by inspection from type 1, which is the type we wish to perpetuate.

Selecting for seed those plants which do have yellow, starchy grains—that is, types 1, 2, 4, and 5 of figure 2—and planting them where they can cross with each other but not with other corn,^a the next year the proportion of each of the nine types that would appear would be as shown in Table VI, column 3. If we make the same kind of selection again the next year the proportions of the nine types would be as in column 4. Table VI shows the results that would be obtained at the end of the sixth generation by this kind of selection in a cross-fertilized crop.

^a Complete cross-fertilization is here assumed. The actual results are intermediate between those shown in figures 2 and 4.

TABLE VI.—Types and their percentages in the descendants of *YySs* for several generations with cross-fertilization and continued selection to type *YYSS*. Regarding *YySs* as the first generation, we have:

Types.	Generations.				
	2.	3.	4.	5.	6.
<i>YYSS</i>	<i>P. ct.</i> 6.25	<i>P. ct.</i> 19.8	<i>P. ct.</i> 31.6	<i>P. ct.</i> 41.0	<i>P. ct.</i> 48.2
<i>YYSs</i>	12.50	19.8	21.1	20.5	19.3
<i>YySs</i>	6.25	4.9	3.5	2.6	1.9
<i>YySS</i>	12.50	19.8	21.1	20.5	19.3
<i>YySs</i>	25.00	19.8	14.0	10.2	7.7
<i>Yyss</i>	12.50	4.9	2.3	1.3	0.8
<i>yySS</i>	6.25	4.9	3.5	2.6	1.9
<i>yySs</i>	12.50	4.9	2.3	1.3	0.8
<i>yyss</i>	6.25	1.2	0.4	0.2	0.1

The type *YYSS* gradually increases until in the sixth generation it constitutes 48 per cent of the crop. This type, together with types *YYSs*, *YySS*, and *YySs*, all of which appear to be the same as

Percentage of each type in each generation indicated by length of vertical line cut off by curves.

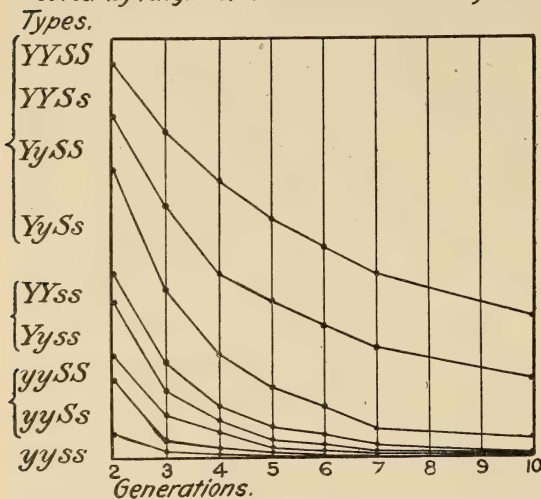


FIG. 3.—Graphic illustration of the effect of mass selection in cross-fertilized species. Selection for type *YYSS*; types so arranged as to bring together those that resemble each other. The proportion of type *YYSS* from generation to generation is shown by the space between the top horizontal line and the upper curved line. It is seen to increase from generation to generation. The proportion of type *YYSs* from generation to generation is indicated by the vertical width of the space between the two upper curved lines. Similarly, the space beginning opposite each type formula indicates the proportion of that type present from generation to generation.

second generation only a small proportion (one-sixteenth) of type *YYSS* is present. In generation six, almost exactly half the population is *YYSS*, while in generation ten this type constitutes about 65 per cent of the whole. The proportion of type *YYSs* present from

YYSS, constitutes 94.5 per cent of the sixth generation. Thus in cross-fertilized crops mass selection to a given type gradually establishes that type, not so rapidly, however, as it does in self-fertilized species, after hybridization.

Figure 3 shows the same thing graphically for ten generations. In this figure the space between the top curved line and the horizontal line at the top of the diagram shows the proportion of the type *YYSS* present from generation to generation. It is seen that in the sec-

generation to generation is indicated by the space between the two upper curved lines. It is seen that this type increases slightly until the fourth generation, after which it gradually decreases. The five types at the bottom of the figure decrease very rapidly from the second generation on, so that by the tenth generation they have almost disappeared, and the population is made up almost entirely of yellow, starch-producing types which are either pure (type $YYSS$) or heterozygote (types $YYsS$, $YySS$, and $YySs$) for one or both of the characters with which we are dealing. Table VI and figure 3 thus illustrate the effect of mass selection on crops which cross-fertilize, and this effect is seen to be a gradual approach toward the type selected.

Evidently the limit of the effect of selection in a case of this kind is reached when practically the whole crop is homozygote for the character selected. No further advance can be made by selection, and it must be remembered that in order to hold the crop at this high degree of excellence selection must be continued, because here and there plants will vary by certain characters becoming latent and thus reducing the general average of superiority in the strain.

The problem of improving cross-fertilized species or varieties by selection to a particular type is complicated by the fact that in plants which ordinarily cross-fertilize we are apt to lose vigor when we get our plants too much alike. That is, these plants have been used to cross-breeding, and when we get our population very uniform, which is only another way of saying get them very close kin to each other, the yield is liable to run down because of this very uniformity. There is some question, therefore, whether in a cross-fertilized crop we should attempt to get great uniformity.

We can partially overcome this difficulty by each year selecting the best individuals we can find and planting them in alternate rows so as to get as much cross-fertilization as possible. In corn the ear-row method of breeding permits this to be done. The methods adopted by some of the best corn breeders in the country at the present time are essentially as follows: Every year they go through the seed plot and also through the cornfield and select the best ears they can find to use in the seed plot the next year. As many ears are selected as there will be rows in the seed plot. In this way there will be the normal cross-fertilization in the seed plot with the resulting vigor that comes from cross-fertilization. Careful account is kept of the yield of each of the rows in the seed plot, so that the breeder may learn what ears selected the year before tend to produce the best yields. This enables him the next year when he goes to the seed plot or the cornfield to select seed to know what types to look for, and it is probably wise, from the standpoint of yield, to select each year two or three types, if not more, pro-

vided they all yield well, so as to insure as much cross-fertilization as possible in the seed plot.

The fact is, we know very little indeed about the relation between yield of corn and type of ear. Prof. A. E. Grantham, of the Delaware Agricultural Experiment Station, recently called the writer's attention to the fact that in communities that have been unaffected by modern ideas about corn breeding, the best ears of corn are usually of the so-called "slick" type. He suggests that this may be a case of the survival of the fittest. Farmers have from year to year selected sound ears for seed, paying little or no attention to type. The prevalence of slick ears may therefore represent a case of the survival of the fittest. In testing local varieties of corn unaffected by modern ideas of selection alongside of the improved varieties, Professor Grantham states that the local varieties yield about as well as the others. The writer can partially verify this statement for southwestern Missouri. On his own farm there is a variety of corn that has been grown there for at least thirty years. The best ears of this variety are decidedly slick; on good land it has yielded 80 bushels per acre. A single year's test of one of the noted improved varieties in comparison with this local one indicates that the improved variety will outyield the other considerably, but it is important to note that the improved variety, although selected for excellence for fifty years, has never been selected for uniformity of type and has not a few slick ears in it.

The amount of careful investigation that this question of relation of type to yield has received is wholly inadequate. It ought to receive careful attention at the hands of our best investigators.

There is another method of breeding open-pollinated crops, like corn, that, while it has not been extensively tried, seems to deserve consideration. This method consists of maintaining two pure strains which are not close kin, and raising each year seed which is a cross between these two varieties and using this seed for the field crop the next year. This method was first proposed by Dr. G. H. Shull^a in an article read before the American Breeders' Association at its Washington meeting in January, 1908. Shull's results have been confirmed by Dr. E. M. East, of the Connecticut Agricultural Experiment Station, whose work is referred to later in these pages. A similar plan was recently proposed by Mr. G. N. Collins, of this Bureau, in a bulletin entitled "The Importance of Broad Breeding in Corn."^b

^a See Report, American Breeders' Association, vol. 4.

^b Since the above was written, Mr. Charles P. Hartley, of this Bureau, has called the attention of the writer to some recommendations made in 1893 and 1894 by Prof. G. E. Morrow and his assistant, Mr. F. B. Gardner, of the Illinois Agricultural Experiment Station. In Bulletin 25 of the Illinois station these investigators say: "The fact that increased yields can be obtained by crossing two varieties is pretty certainly

A representative of the Office of Farm Management several years ago reported that in a certain community in one of the Western States farmers generally planted white and yellow corn in alternate rows in their seed patches. In this way they were sure of getting the vigor that comes from hybridization in the corn to be used for the general field crop the next year. Some of the farmers simply planted their whole field in alternate rows of yellow and white corn, and the next year used seed selected out of this field for planting. The next year they would go back again and get pure yellow and pure white corn from some outside source and start over again, but this is a crude method which gets advantage of the hybridization only every other year. A better plan would be to get two good varieties of corn, both known to be adapted to the conditions, and plant a seed patch somewhat more than twice as large as needed to produce seed for the fields the next year, planting the two varieties in alternate rows in the seed patch. In one-half of the seed patch one of these varieties is detasseled and in the other half the other variety is detasseled. On both sides of the seed plot the detasseled stalks would bear only hybrid grains. On the other hand, the stalks that were not detasseled would be fertilized by pollen from stalks of the same variety, except in the middle of the patch, where there would be some cross-pollination between the two varieties. At harvest time pure seed of the two varieties is selected for the next year's seed plot from the extreme sides of the plot, where there has presumably been no cross-fertilization between the two varieties, while seed for the general field crop is selected from the detasseled stalks

established, and a few farmers are changing their practice accordingly. This is quite easily done, by planting in one row one variety, and in the next another variety, and removing the tassels of the one as soon as they appear. The ears forming on the rows having the tassels removed will be fertilized with pollen from the other rows, thus producing a direct cross between the two varieties. The seed should be selected from the rows having the tassels removed, and the experiments indicate that it will pretty certainly give a larger yield than the average of the parent varieties when planted under like conditions."

In a comparison of five crosses with the average yields of their parents the average increase in yield due to having crossbred seed in the experiments above referred to was 9.5 bushels.

Again, in Bulletin 31 of the Illinois Agricultural Experiment Station the same authors make this recommendation: "Farmers can produce crossbred seed in considerable quantities in the following manner: Plant with one variety in one planter box and another variety in the other. Remove the tassels of one variety before they begin to shed pollen, and the shoots of the same will be fertilized with pollen from the other variety, thus producing a direct cross. The seed should be selected from the rows from which the tassels have been removed."

In three out of four comparisons between crosses and their parents reported in the bulletin last referred to the crosses outyielded the parents, the average increase being 2.3 bushels per acre in favor of the crosses.

from the whole plot. This method would take advantage of the well-known vigor which arises when two varieties of corn are crossed.

Shull has recently proposed a plan somewhat similar to the above, and one which is really an improvement on it in one respect, but not so good in another.^a He suggests using two pure strains, planting one of them off by itself to get pure seed of it for the seed patches the next year, while at the same time another seed patch for growing field seed is planted of alternate rows of the two varieties. In this patch all the stalks of the variety grown alone in the other patch are to be detasseled. All the seed produced by the detasseled stalks will be heterozygote, while all the seed on the remaining stalks will be pure bred of the other strain from that planted alone in the smaller patch. The principal difficulty with this plan is that of finding isolated spots for two seed patches instead of for one, as in the plan in which the two varieties are both planted in alternate rows in one patch. In Shull's plan the two strains could be kept practically pure; in the other plan they would mix to a slight extent.

HYBRIDIZATION AND SELECTION.

We have been considering only the effect of selection without deliberate hybridization or cross-fertilization, except such as occurs naturally in certain of the crops considered. We shall now consider the application of artificial cross-fertilization and subsequent selection to the art of improving farm crops.

As in the case of selection alone, the methods and results differ for vegetatively propagated, close-fertilized, and cross-fertilized crops.

VEGETATIVELY PROPAGATED CROPS.

It is perhaps easier to secure the advantage of hybridization in vegetatively propagated crops, such as fruits, berries, potatoes, hops, and sugar cane, than it is from those crops that reproduce from seed. The reason for this is that some of the heterozygote forms which occur in the first generation of the hybrid may be highly valuable, and these heterozygote forms can be propagated true to type because they are not propagated from seed. For instance, suppose we cross two varieties of apples or potatoes and get in the first generation a plant from which can be made a valuable new variety. All that is necessary is to propagate this new variety by cuttings.

In the case of potatoes very little hybridizing has been done. The seedling plants do not attain their full development until propagated from the tubers for two or three years. It is therefore necessary gradually to eliminate the poorer stocks and to grow for some time a good many of the forms which result from crossing, to see whether or not they are valuable.

^a See Report, American Breeders' Association, vol. 5.

It must also be remembered that nearly all crops which are propagated vegetatively belong to the class of crops which naturally cross-fertilize; so that when we make a cross between two of them we are really crossing things that are themselves many times hybrid. For instance, a Baldwin apple tree is heterozygote for a good many of its characters. For this reason it produces many kinds of pollen and ovules, and when we use the Baldwin in a cross we get numerous different varieties in the first generation, while if the two varieties used in the cross were completely homozygote for all their characters all the first-generation hybrids would be alike.

SELF-FERTILIZED SPECIES.

The principles involved in the hybridization and subsequent selection to type of close-fertilized species, like wheat and oats, have already been stated in more or less detail, but some additional points need to be brought out. In utilizing hybridization in close-fertilized crops the first problem is to select suitable forms for hybridization. Sometimes these forms are already at hand and well known. The real object to be accomplished by hybridization in this case is to make use of the law of recombination, by which we can bring together in one variety certain valuable characteristics which are found scattered among two or more varieties which we may have at hand or can secure. Take, for instance, the problem which presented itself, while the writer was agriculturist at the Washington Agricultural Experiment Station, in connection with wheat growing in eastern Washington. When the writer first went to Pullman, where the experiment station is located, the farmers had been growing wheat in that section for twenty-five or thirty years. They had tested many hundreds of varieties, but found very few of them adapted to local conditions. Only three varieties had at that time come into general use, and these three were each more or less restricted to definite areas of different rainfall. For instance, where the rainfall was 10 or 12 inches almost the only variety grown at that time was Bluestem (not the hairy chaffed Bluestem of the middle Northwestern States). This was grown for two reasons. In the first place, it was one of the very few varieties found that would grow tall enough to cut with so little rainfall. In the second place, it produced a very superior quality of flour, and millers paid about 3 cents a bushel more for it than for other varieties. But this tall-growing variety could not be grown where the rainfall was 20 inches or more, because it would fall down if the season was at all unfavorable. Where the rainfall was about 18 inches a variety of club wheat known as "Red Chaff" was very widely grown, while

in those sections where the rainfall was 22 inches or more the prevailing variety was another club wheat known as "Little Club."

The growers of Red Chaff gave as their reasons for using this variety that it stood up better than Bluestem and yielded more than Little Club, while the growers of Little Club stated that this was the only variety they had ever found that would stand up and hold its grain under their conditions.

It happens that all three of these varieties are spring wheats, but long experience has shown that sowing them in the fall would, in favorable seasons, produce yields 30 to 60 per cent greater than spring sowing. Hence, all three varieties were generally sown in the fall, but they would frequently freeze out to a greater or lesser extent. There was therefore an insistent demand for winter wheat. The writer had collected from various parts of the world an extensive series of winter wheat varieties, and in 1899 a large number of these varieties had been grown for five years. Many of them were perfectly hardy and made enormous yields in favorable seasons, but they were inclined to straw-fall and to shatter their grain as soon as they were ripe; so that it did not seem advisable to recommend any of them to the farmers.

At that time Mendelian principles were unknown in this country and had been forgotten in Europe, so that the writer had intuition alone to guide him in his attempts to produce a variety of wheat adapted to local conditions. By chance these intuitions proved to be correct and led to the discovery of the law of recombination previously stated. Fortunately, the work proceeded from the beginning just as it would have done had the writer had full knowledge of the law of recombination, for the law was discovered in time to use it as soon as it could have been used in this work.

Eleven of the best yielding winter varieties were crossed with the Little Club and the Red Chaff varieties (the Bluestem could not be successfully grown at Pullman, where the rainfall was about 22 inches). Among the first-generation hybrids there were, therefore, eleven kinds. The seed of each hybrid plant was saved separately, so that the next year we had as many plots as we had hybrid plants the year before.

The object of this hybridization work was to combine the winter hardiness of one class of varieties with the stiff straw and the tightly closed chaff of the other varieties. We now understand why this combination succeeded in every one of the crosses, so that from each of them resulted new and fixed varieties of wheat combining the characteristics mentioned. As was to be expected, some of the new varieties proved to be much more productive than others.

The writer severed his connection with the Washington Agricultural Experiment Station at the beginning of 1902, but his successor and his assistants continued the work with the hybrid wheats, and this work is still in progress, being conducted by Mr. C. W. Lawrence, of the Washington station.

Three of these hybrid varieties (which had been fixed by proper selection, methods of which are outlined below) were distributed in small quantities to the farmers in the fall of 1907, after having been carefully tested at the experiment station as to their yielding power. In the fall of 1908, 39,000 acres of these new varieties were reported as being sown by the farmers in eastern Washington. In two more years there will doubtless be seed enough for all.

The case just cited illustrates one in which hybridization furnishes a means of securing new and valuable varieties, namely, the case where certain valuable characteristics are found in different varieties and it is desirable to unite these characteristics. Such cases would exist at most plant-breeding stations. Doctor Nilsson, at Svalöf, has made extended use of these principles in producing new varieties of cereals at his station. The first task is to select the varieties having desirable characteristics. Frequently some of the characteristics will be found in varieties that are otherwise worthless, so far as their use as field crops is concerned, so that in breeding work a variety should not be rejected because of a single weakness. It is legitimate to use an inferior variety in crossing, provided it has some valuable characteristics.

In working with self-fertilized crops the principles involved for the first two years are exactly the same as those in cross-fertilized crops illustrated in Table VI. The first generation of the hybrid is heterozygote for all those characteristics in which the two parent varieties differ. Where the parents differ in a great many respects the problem becomes quite complex, for the number of types that will be produced in the second generation is equal to 2^n , n being the number of points in which the two parents differ. Thus, when they differ in one particular, that is, when we have one pair of allelomorphs to deal with, there are two distinct types in the second generation of the hybrid. If the parents differ in two respects, we have $2^2=4$ distinct types in F_2 (the second generation of the hybrid). Three differences give $2^3=8$ types, and so on. The figures given above assume that in each pair of allelomorphs there is complete dominance, so that the heterozygotes can not be distinguished from the pure dominants. If the heterozygotes can be distinguished, then the number of visibly different types in the second generation is 3^n . In fact, in so far as their content of hereditary characters is concerned there are always 3^n types in the second generation when the

varieties crossed differ in n particulars. In many cases we can neglect a great many of these differences, because they are immaterial and deal only with those character pairs which are important. Table VI shows what occurs when the parents differ in two respects. The first generation is heterozygote with respect to both character pairs. In the second generation nine types occur in the proportion shown in Table VI.

In the third generation we get a different result with self-fertilized plants from that obtained in cross-fertilized plants, because in self-

Lengths of vertical lines cut off by curves show proportion of types in each generation.

Types.

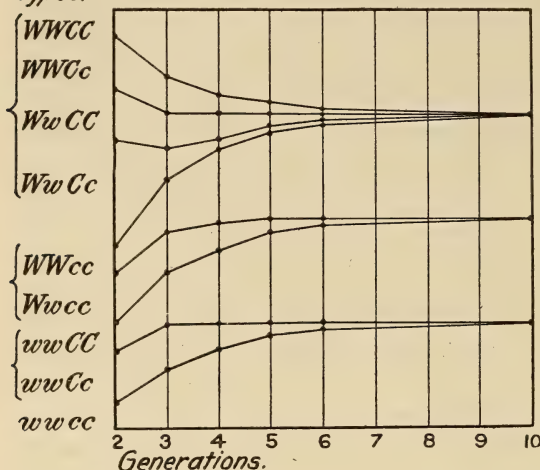


FIG. 4.—Graphic illustration of ten generations of a hybrid in a self-fertilized species without selection to type: W , winter character; w , absence of W (i. e., spring character); C , club character (short, thick heads); c , absence of C (i. e., long-head character). Types arranged so as to bring together those that resemble each other. The space between the top horizontal line and the uppermost curved line shows the proportion of type $WWCC$ present from generation to generation, and the space beginning opposite each type formula shows the proportion of that type. The population ultimately consists almost entirely of the four homozygote types present.

between a long-headed winter wheat and a club or short-headed spring wheat. In the second generation we get the usual nine types, as seen at the left of figure 4, where W = winter character, w = spring character, C = club heads, and c = long heads. The nine types are arranged in figure 4 so as to bring together those which appear to the eye to be alike. Thus the types $WWCC$, $WWCc$, $WwCC$, and $WwCc$ are all winter clubs, since W is dominant over w and C is dominant over c . $WWcc$ and $Wwcc$ are long-headed winter wheats, $wwCC$ and $wwCc$ are spring clubs, while $wwcc$ is a long-headed spring type.

fertilized species a heterozygote when it makes seed breaks up into one-fourth pure dominants, one-half heterozygotes, and one-fourth pure recessives; while with open-pollinated species the proportion of heterozygotes produced by heterozygotes will be larger than one-half, because of the introduction of foreign pollen.

Let us first consider what occurs in self-fertilized species if we make no selection at all among the progeny of the hybrid. Figure 4 shows what occurs in this case. Suppose the plant with which we are dealing is a hybrid

The relative proportion of each of these nine types for a series of generations, from the second to the tenth, is shown in the diagram of figure 4. For instance, the proportion of type *WWCC* is indicated by the space between the top horizontal line of the diagram and the upper one of the curved lines. The generations are indicated by the figures at the bottom of the diagram. In generation two the space for type *WWCC* is narrow, constituting only one-sixteenth of the second generation. But this type increases from generation to generation until by the tenth generation it is practically one-fourth of the population; that is, when there is no selection to type.

Type *WWCc* is seen to decrease from generation to generation, as indicated by the space between the two upper curved lines. This space gradually becomes narrower, so that it has practically disappeared by the tenth generation. The space beginning opposite each type formula shows what happens to that type. It is seen that the four homozygote types *WWCC*, *WWcc*, *wwCC*, and *wwcc* gradually increase in proportion while all the heterozygote types decrease. By the tenth generation the whole population consists practically of the four homozygote types, each of them constituting practically one-fourth of the population. Only small amounts of any of the heterozygote types remain in the tenth generation. Of these four homozygote types, two of them will be just like the two parents, as far as the characters we are considering are concerned. The other two will represent new combinations of the characters under consideration; the new types are (1) winter character with club heads and (2) spring character with long heads. We may therefore in such cases (i. e., with self-fertilized crops) secure our hybrid and plant its seed for several years without any selection at all, then select out the type we want and it will be almost entirely pure; that is, nearly all the plants selected will reproduce true to type as far as the characters wanted are concerned. Then selecting individual plants of the type wanted we can quickly get plants that are homozygote with reference to practically all their characters by planting the seed of each plant separately and observing which of them do reproduce true to type.

These fixed forms which occur in the progeny of hybrids are sometimes mistakenly called "mutations." They are in no sense mutations of the sort comprehended by that much misused term as it is at present understood. They are simply recombinations of characters which, before the hybridization occurred, existed in different combinations.

After these fixed forms are obtained the same laws apply to their selection as have already been described under the effect of selection on close-fertilized forms. Generally speaking, we can not modify

them by selection, but selection may be valuable as a means of holding them up to a high standard.

Reverting again to the hybrid produced by crossing long-headed winter wheat with a club-headed spring wheat we shall now consider the effects produced, first, by mass selection and, second, by individual selection in the progeny of such a hybrid. Figure 5 shows the result of mass selection for the winter club type. Since both the winter character and the club character are dominant in this cross, four of the nine types occurring in the second generation will appear to be winter club wheats. These are the upper four types of figure 5. The other five can be distinguished at once, because they will either show the long-head character or the spring

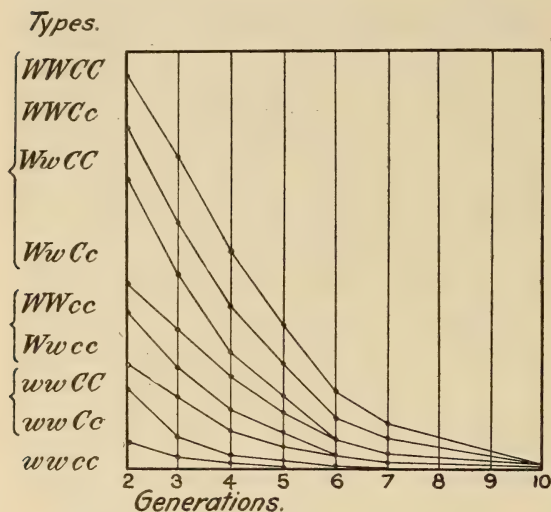


FIG. 5.—Graphic illustration of ten generations of a hybrid in a self-fertilized species selected for type *WWCC*. The letters and spaces between curves have the same significance as in figure 4.

character, *w* for the spring character, *C* for the club character, and *c* for the long-head character. The first of these four types is already fixed and will reproduce itself faithfully. The others are heterozygote with reference to one or both character pairs, and will consequently the next year produce some progeny which will be either spring or long-headed wheat, or both. Suppose, now, that in the second generation we discard everything except these four types. Figure 5 shows what the result will be. The diagram of figure 5 is easily interpreted if we understand that the space between the top horizontal line and the uppermost curved line represents type *WWCC*, the space between the two uppermost curves represents type *WWCc*, and so on. It is seen that in the third generation, type *WWCC* has increased greatly in

To determine whether or not a wheat is winter or spring in character it should be planted in the spring. If it makes a crop the same season it is a spring wheat. If it waits until the next season before it heads out it is a winter wheat. The four types in the second generation which appear to be winter club wheats are those having the constitution *WWCC*, *WWCc*, *WwCC*, and *WwCc*, in which *W* stands for the winter

proportion. Type *WWCc* about holds its own until the fourth generation, after which it decreases. The same is true of type *WwCC*, but type *WwCc* decreases rapidly from the second generation onward. At the end of ten generations practically the whole population is of type *WWCC*, which is pure winter club wheat, with a very small admixture of other types. This shows the effect of mass selection after hybridization in the case of self-fertilized crops. The result is a much more rapid approach to the one type selected than occurs in the corresponding case with cross-fertilized crops as shown in figure 3.

The effect of individual selection, i. e., selection in which the seed of the individuals selected is kept separate, is shown for self-fertilized crops in figure 6. In this figure, as in the preceding, the space beginning opposite each type symbol shows the proportion of that type from generation to generation. In this method of selection we save each second-generation individual which appears to be of type *WWCC*. This includes all plants of types *WWCC*, *WWCc*, *WwCC*, and *WwCc*. The seed of each plant is kept separate. In the next generation we save seed only from those rows or plots in which there has been no splitting up. This gives us at once the type *WWCC* in pure and fixed form. This is shown in figure 6, where the space representing type *WWCC* occupies the whole diagram beyond the third generation.

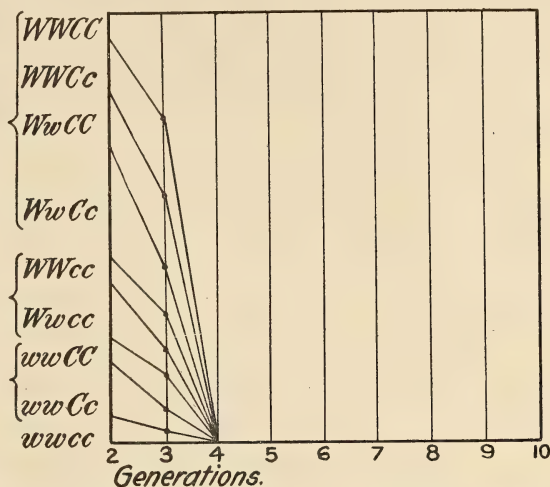


FIG. 6.—Graphic illustration of the effect of individual selection in a self-fertilized species on progeny of the hybrid *WwCc*. After the third generation the race is pure for the selected characters (both dominant in this case). The letters and spaces between curves have the same significance as in figure 4.

CROSS-FERTILIZED SPECIES.

The problem of utilizing hybridization in the production of new forms in cross-fertilized species which are propagated from seed is somewhat complicated by the fact that the individuals to be used in crossing may themselves be heterozygote for many characters. Diversity in such species differs from that in self-fertilized species in this respect: In the latter we usually have in homozygote form all the combinations possible of the characters found in the group,

while in cross-fertilized species we have the same combinations, but not in homozygote form. In self-fertilized species, when a desired combination is not at hand, we can easily produce it and get it in fixed form. In cross-fertilized species, if the desired combination is not at hand, we can get it by crossing, but can not be sure of keeping it unless it is a form that can be propagated vegetatively, such as berries, tree fruits, and potatoes. The best we can do in cross-fertilized species which are propagated from seed is to make a cross with a view to getting a certain desired combination of characters and then select the desired type until we get a fairly constant strain of it. The results that follow such selection have already been explained under the head of "Cross-fertilized species," page 36, and illustrated in figure 3.

It has already been hinted that in cross-fertilized species we should not try for too great uniformity, as such uniformity in cross-fertilized species usually goes with weak development. If by crossing and subsequent selection we can get two forms, each of which is homozygote for the same desirable characters but heterozygote for other characters which are of no importance, and then plant them so that the two forms will cross freely, we shall probably have the nearest approach to the desired end attainable in such forms.

MENDELIAN ANALYSIS OF HETEROZYGOTE RACES.

When an individual which is heterozygote for a given pair of allelomorphs is self-pollinated it breaks up in the next generation into three forms, or types, two homozygote and one heterozygote. Let our pair of allelomorphs be represented by Aa . With self-pollination we have in the next generation one-fourth AA , one-half Aa , and one-fourth aa . That is, one-fourth of the seed produced is homozygote for A , one-fourth for a , and one-half of it is heterozygote, Aa . Hence, in such species as apples, pears, strawberries, and cassava, which do not ordinarily reproduce true to seed because they are heterozygote, usually for many of their characters, if we self-pollinate them, in the next generation we get many forms that are homozygote for some characters. If the species will endure continued self-pollination it is clear that we could in eight or ten generations break up any variety of this kind into homozygote types that would reproduce true to seed. In fact, there are a good many varieties of some of the species just mentioned that do reproduce practically true from seed. The Royal Anne cherry of Oregon and Washington is a case in point. Many of its seedlings can hardly be distinguished from the original variety. Where it is possible to secure these homozygote forms by this process of breaking up into

pure races, a process which we may call Mendelian analysis, such forms might be of great importance to the breeder. They might render possible the deliberate combination of highly desirable characteristics existing in different varieties. Some very interesting work of this kind has been done. Prof. S. M. Tracy, working under the direction of the writer, has thus obtained three races of cassava which reproduce practically true to seed. They are now being used in an attempt to propagate this crop from seed instead of from cuttings. If the attempt is successful, and it promises to be so, it will permit a considerable extension of cassava culture into latitudes in which it is not practicable to propagate cassava from cuttings, because of the difficulty of keeping the cuttings over winter.

In Volume V of the Annual Reports of the American Breeders' Association, Dr. W. T. Macoun, of Canada, reports some very interesting facts regarding the seedlings of the Wealthy apple. There was probably some cross-pollination in this case, but the seedlings give very plain evidence of the parentage of this important variety of apple. This is an important and nearly virgin field of investigation, and more work of this kind will be looked for with interest.

HETEROZYGOTE CHARACTERS.

In some crosses, or hybrids, characters appear in the first generation of the cross that were not apparent in either parent. These characters may belong to either of two classes. First, they may be due to the heterozygote nature of the hybrid. Characters of this class can be taken advantage of by the breeder only when the plant concerned can be propagated vegetatively. In crops propagated from seed a character which is due to the heterozygote nature of the plant which bears it will appear in the next generation in only half the progeny. Such characters can not be fixed by selection; at least no one has as yet succeeded in doing so, and it is highly improbable that it can be done.

The most common type of such characters is the well-known vegetative vigor seen in many hybrids. It is not unusual in sorghum fields to see here and there a stalk which is much larger and taller than the rest of the field. Investigation has shown that these plants are hybrids. The writer has noticed in his work with hybrid wheat that the first-generation hybrid is much more vigorous and stronger growing than either of the parents as a rule, though this vigor in hybrid wheats is not so marked as it is in sorghum. In corn it is especially marked. Dr. G. H. Shull by the close breeding of two varieties secured practically homozygote strains of them, which were then crossed. The yield of the hybrid was about five times that of the attenuated self-fertilized pure strains. It should be

remarked that the pure strains of corn, because of the close inbreeding, had become very weak yielders, while the hybrid yielded an exceedingly large crop.

Dr. E. M. East, of the Connecticut Agricultural Experiment Station, in a similar manner produced on small plots at the experiment station yields of corn exceeding 200 bushels per acre from hybrid seed. Here is an important point for the corn breeder.

A good deal of effort has been made to secure uniformity of the ears in corn by a system of rather close breeding. This method will give the desired uniformity, but the close breeding in a species naturally cross-fertilized is likely to lead to lessened yields. Is it not better to breed for excellence, taking care not to breed too closely, and let uniformity take care of itself? A method of using two strains of corn in the breeding plot in order to secure hybrid seeds for the field crop has already been described.

Increased vegetative vigor does not occur in all crosses. Before recommending the cross-breeding of any particular crop in order to secure increased vigor, the fact that in that crop the desired results will follow should be determined.

The following are other cases of characters which occur only in heterozygote form. In the cross between Black Andalusian fowls and a variety of White Andalusians having black splashes on the feathers, here called White Andalusians for convenience, the heterozygote is blue. If these blue fowls be mated with each other one-fourth of their progeny is black, one-half blue, and one-fourth white. If Blue Andalusians are desired, 100 per cent of blues can be obtained only by mating blacks and whites.

According to Professor Bateson, exactly the same phenomenon occurs in the Bredas, a breed of fowls found in Holland.

A similar case occurs in the cross between a certain red primrose and a certain white primrose, reported by Professor Bateson. The heterozygote is purple and is known to the trade under the name of "Imperial Primrose." Fifteen years of persistent selection has failed to cause this primrose to come true to seed. Every year one-fourth of its seed produce plants having red flowers, one-half of the seed produce plants having purple flowers, while the remaining one-fourth have white flowers.

Dr. G. H. Shull found a mottled character in the seed coat of certain first-generation hybrid beans which proved to be a heterozygote character; that is, when it appeared it was always heterozygote and would then reappear in only half of the plants whose seeds were mottled. Prof. R. A. Emerson, of the University of Nebraska, found the same character in beans, as did also Professor von Tschermak, of Vienna, and Mr. Locke, of Ceylon.

Cases like those cited seem to be due to the presence of two characters in different varieties which are not manifest in those varieties; but when brought together by hybridization they react on each other in some unknown manner so as to give rise to a new character. At the same time they form a Mendelian pair and separate again on the formation of gametes. Perhaps in such cases two chromosomes, which meet to form a bivalent in the reduction division, each throw off into the cell a different chemical substance, and these two substances, by reacting on each other, give rise to the new character. When these two chromosomes are not together in the same cell the character does not appear.

Most of such characters are probably reversions to lost characters. The fact that there are mottled races of beans like those produced by Shull and others, and which reproduce true to seed, is in favor of this suggestion. In these mottled beans which reproduce true to type we may suppose that each of the chromosomes in question produces both of the chemical substances which we have supposed give rise to the character. If this is the case, then nonmottled varieties of three types could arise from a mottled variety by the loss on the part of the chromosomes producing the two necessary substances of the power of producing one or the other or both of these substances. If in one variety of beans one of these substances and in another variety the other substance is missing, crossing the two varieties would cause the lost character to reappear. This matter will be considered more fully when we are considering the subject of latency of hereditary characters.

Thus far we have considered only those new characters arising in crosses and which appear only in heterozygote form. There is a second class of characters arising in crosses that may be fixed by proper procedure. In working with gillyflowers Bateson and his coworkers found an interesting case of this kind, which will be considered more fully under the head of latency and need only be referred to briefly here. In crossing a certain white variety with a cream-colored variety the progeny produced red flowers, and in the second generation some individuals were obtained having red flowers and reproducing true to seed. Evidently this result was due to the fact that two characters neither of which produced any effect when alone but when brought together gave rise to a visible character did not form a Mendelian pair and could consequently both be transmitted together.

The reason why a character of this type can be fixed is seen in the following. We have assumed that the new character arises by the bringing together of two other characters that are not allelomorphic to each other; that is, do not form a pair which must separate on the formation of gametes. If we call one of these characters *A*, its

absence a , the other B , and its absence b , the first-generation hybrid is constituted thus, $AaBb$. This hybrid produces four types of gametes, namely, AB , Ab , aB , ab . An ovule of the type AB uniting with pollen of the type AB gives $AABB$, a homozygote strain in which the new character is fixed. While such cases as this are not common, they may occasionally represent important advances in breeding. It is therefore well for the breeder to understand them. Several such cases have been found. They also probably represent reversions to lost characters, at least in most cases.

Characters may also appear in the second generation of a hybrid that were not apparent either in the first generation or in either of the parents. This is especially the case when a character is hypostatic in one of the original parents of the cross; that is, when it is covered up or hidden by some other character. A case in point is the appearance of brown beans in the second generation of the cross between black and white, reported by Shull. Here the brown is hypostatic to black, i. e., obscured or hidden by the black, in the black parent. Letting B represent black, b its absence, D brown, and d the absence of brown, the formulæ for the black and white forms and the hybrid between them is—

Black, $BBDD$.

White, $bbdd$.

Hybrid, $BbDd$.

The gametes produced by this hybrid are BD , Bd , bD , and bd . The union of an ovule of the type bD with pollen of the same type gives $bbDD$, a brown type.

Similar cases are known in animals.

POSSIBILITY OF ENTIRELY NEW CHARACTERS.

While most apparently new characters that arise in crossing are probably reversions to lost characters, it is easily conceivable that entirely new characters might arise in this manner. It seems probable that some cases of reversion are due to reaction between chemical substances, one of which is derived from one parent and the other from the other. These substances are probably produced in the cells of the respective pure strains before the cross; but they produce no effect because they are not both present in the same cells. It is conceivable that in some races there may have occurred evolutionary changes that result in considerable modification of the chemical contents of the cells but which produce no visible effect on external characters. In two related races these evolutionary changes may be quite different, and when we cross two strains that have been separated for some thousands of generations we may get, by reactions between substances that in the respective

pure races are of no effect, entirely new characters which thus seem to appear suddenly, but which in reality may have been thousands of years in developing. Characters arising in this way would appear only in heterozygotes if the two factors brought together happened to form a pair. But if they did not form a pair the new character would be capable of being fixed.

Some phenomena have occurred, especially in crosses between distinct species, which probably belong in the class here considered, though not enough work has been done in this direction to make this entirely certain.

RECIPROCAL CROSSES.

If in one cross we use the pollen of race *A* on the stigmas of race *B*, while in another cross we use the pollen of race *B* on the stigmas of race *A*, these two crosses are said to be reciprocal to each other. Ordinarily such crosses give identical results. In his work with hybrid wheats at the Washington Agricultural Experiment Station the writer made reciprocal crosses in three instances, and in each case the results of the reciprocal crosses were identical. There are cases, however, where reciprocal crosses give different results. In some species the plant produces more than one kind of pollen and only one kind of ovule, as Correns found in *Bryonia*. He crossed a diœcious species with a monœcious species. When he used pollen of the diœcious species the hybrids were male and female in equal numbers, but when he used the pollen of the monœcious species the hybrids were all female. A number of other cases are known which may be explained on a somewhat similar basis. In a few cases differences have appeared in reciprocal crosses for which no explanation has been found. The plant breeder should make a careful record of any such cases coming under his observation, as they may lead to important advances in our knowledge of the principles of heredity.

EVOLUTIONARY CHANGES AND THEIR RELATION TO PLANT BREEDING.

While a great deal of study has been given to the general subject of evolution, actual knowledge of how and why evolutionary changes occur is very limited. The discussion this subject has received has been largely theoretical, and usually in support of some theory as to the manner in which such changes occur.

We may perhaps distinguish two or more classes of evolutionary changes. A complex organism is provided with many hereditary characters—that is, characters which appear in successive generations. These characters may change in the manner of expression. For instance, a species having purple flowers may change with reference

to the shade of coloring, or a variety may change in size, and so on. Again, a character may become latent, possibly lost entirely. Thus, a purple-flowered species by the loss or latency of a factor for purple, may become red. Again, a red flower might become purple by the revival of the latent factor for purple.

It is probably safe to say that most evolutionary changes are of the classes mentioned in the preceding paragraph. Take, for instance, the color of wild mammals. Nearly all mammals, so far as they have been studied, have the same factors for color. The differences in the colors of the different species have come about simply by modifications in these same factors. Yet, some evolutionary changes result in the development of new characters. Beards on grasses must at one time have been new organs. But changes of this kind are comparatively rare, and occur so seldom that we can take little cognizance of them in practical breeding work.

As stated before, we do not know the cause of these changes. One school of biologists maintains that evolutionary changes are slow and gradual, another that they take place by instantaneous steps, which may be large or small—that is, that they are “discontinuous.” We are more interested here in the amount of change that may occur in a given time than in the manner in which such changes take place. The important point is that when evolutionary changes do occur they are usually permanent changes, and the new forms resulting are subject to the laws of selection and hybridization which have already been outlined. That these permanent changes do occur can not be questioned. That in general they are merely changes in hereditary characters already present is equally certain. Doctor Nilsson in his work with the cereals at Svalöf has many times taken an unselected lot of seed from a standard variety of field grain and found it in the main to consist of a large number of fixed types differing from each other in various ways. When the same character is studied throughout the numerous strains that occur in a field it is found to present nearly every possible gradation in different strains, but generally speaking in each of the strains the gradation found is fixed.

Jennings, in his study of *Paramecium*, found in wild cultures almost an indefinite number of strains, each differing permanently in size, and these differences undoubtedly are due to permanent changes of hereditary characters, as in the case of Nilsson’s cereals. Jennings’s investigations indicate that there might be found in *Paramecium* almost every gradation in size, but that the size of each particular strain is fixed.

The principal relation of these changes to the work of the plant breeder lies in the fact that a crop as grown under field conditions will

usually consist of a large number of strains which differ from each other on account of evolutionary changes which have occurred in the past, and the breeder can by selection secure the strains which are of greatest value.

A few instances are known in which important changes have been brought about by persistent selection. De Vries, by continued selection from a 13-rayed strain of *Chrysanthemum segetum*, was finally able to produce a double-flowered variety. Burbank found a single specimen of California poppy which had a scarlet line on one of its petals. By persistent selection from this plant he was able to get a scarlet poppy. Cases of this kind are not understood, yet they are important from the standpoint of the breeder. They show that we have much yet to learn in this important field. It may be stated that scarlet-flowered California poppies occasionally occur in nature. This fact shows that at least part of the species has the scarlet color factor. It is probable, therefore, that Burbank started with a plant having this factor, and by selection merely eliminated other color factors.

PLACE EFFECT.

It is a well-known fact that when a crop is moved to a locality which is radically different from that in which it was previously grown it sometimes behaves in a surprising manner, presenting unlooked-for variations. This subject has not been studied nearly as much as it ought to be. We really do not know the behavior of the variations which occur under such conditions, because so little attention has been given to them.

Take, for instance, the case of the tomato in southern climates. Some of the standard varieties of tomatoes present very peculiar modifications when seed grown in the North is planted in the far South. The first year the fruit is normal and resembles the fruit that would have been produced in the North; but if seed of the southern-grown fruit be saved and planted, the next year the fruit is of a very different character and remains so from generation to generation under the new conditions. The writer is informed by Mr. W. W. Tracy, sr., of this Bureau, that when the seed of these transformed tomatoes is taken back to the North and planted, while the first year it grows the southern type of tomato, the next year it reverts to its northern form. Cases of this kind are well worth more attention than they have received.

It is to be noted that in the case of the tomato just referred to the same change occurs in all the individuals. In this connection, some work recently done by Dr. Albert Mann, of this Bureau, is of special interest. Although the results are as yet unpublished Doctor Mann kindly permits me to refer to them.

Three years ago he obtained from Doctor Nilsson, of Svalöf, a number of the pedigreed or pure-line strains of barley grown at that station. Seed of five or more of these were sent to thirty-eight localities throughout the country in 1907, representing nearly two hundred tests. In all cases more or less transformation occurred in each of the strains under investigation. Generally speaking, every individual of a given strain went through identically the same transformation in the same locality. The results obtained the second year on some thirty locations indicate that the changes made by these plants are permanent as long as they are grown under the new conditions.

In several instances it was found that a given strain did not behave alike, part undergoing one modification and part another. A careful study of one of these cases revealed the fact that one end of the plot was on sandy soil and the other on loam and that all the plants at the same end had suffered the same change.

Doctor Mann has called my attention to the important fact that these changes suffered by pure lines when taken to a radically different environment from that to which they had been accustomed seem in no way to be adaptive changes. They are apparently not adjustments to the new conditions, but are changes caused by the new conditions. Apparently, they may be advantageous or disadvantageous to the plant under its new surroundings.

It is easily seen that by studying this question with types of plants from which all other kinds of variation have been eliminated, results of fundamental importance may be obtained. The conclusions, which are at least indicated by the very meager data at hand, are that these new-place effects produce similar results on similar individuals, that they are permanent under the changed conditions, and that they are fortuitous in character. It is by no means established, however, that these conclusions are general. This is evidently an important and nearly virgin field for investigation.

NON-MENDELIAN CHARACTERS.

The only case known to the writer of a non-Mendelian character which has been clearly made out and for which the method of inheritance has been determined is one recently published by Dr. Erwin Baur, of Berlin, and which relates to the method of inheritance of the white margin of certain leaves.^a The white-margined plants produce only pollen and ovules carrying the white tissue character. But when these plants are crossed with ordinary green plants the new individual thus formed is capable of producing both kinds of tissue. It would

^a Since the above was written the publication of Castle's monograph on inheritance in the rabbit has been made by the Carnegie Institution. Had this publication appeared earlier it would have received extended notice in these pages.

appear that in the cross-fertilized ovule, part of the cytoplasm of the cell carries the tendency to develop green tissue and part the tendency to develop white tissue. If at any cell division one of the daughter cells should happen to receive only cytoplasm of a certain kind then the tissue descended from that daughter cell will be either pure white or pure green, as the case may be. Plants originating from this cross between white and green are thus called mosaics. A leaf or bud originating on the line of contact between the tissues will be white on one side and green on the other. If it originates wholly from white tissue it will be pure white; if wholly from green tissue it will be pure green. Occasionally, however, the white tissue on the stem of such plants may extend as a thin surface layer over the green tissue. A bud coming through such a layer will be composed of green tissue within and a thin layer of white tissue without, and this bud gives rise, by division and propagation, to a new white-margined plant.

Another case which should be mentioned here is that of the inheritance of ear length in rabbits studied by Prof. W. E. Castle, of Harvard. The cross between long-eared and short-eared rabbits had ears intermediate in length, and their progeny were like the hybrid in this respect. In this case the mechanism of inheritance is not clear; and it is barely possible that it is simply a very complex case of Mendelian inheritance.

In a great many crosses between very distinct species we do not get strictly Mendelian phenomena and we do not know exactly why. It is highly probable, however, in the writer's opinion, that the reason is to be sought in the following. Most of the organs and parts of an organism are developed as the result of the interaction of a good many factors which are Mendelian in nature. For instance, the development of horn tissue in cattle may be the result of the interaction of three or four or even more chemical substances arising from different organs in the cell. Now, if in two races of cattle we find a difference in only one of these chemical substances, then the differences between the two races would behave as a simple Mendelian character; but if there were differences in all the substances concerned we should have an exceedingly complex case of Mendelian inheritance, the unraveling of which would require such large numbers of progeny from hybrids that it would be practically impossible to determine the nature of the inheritance in the case. The writer is of the opinion that the lack of simple Mendelian characters in species hybrids is partly of the nature here outlined. In some species crosses apparently wide departures from Mendelian principles occur. Take, for instance, the cross made by Burbank, resulting in the *Primus* berry. Here there was wide diversity in the first-generation hybrids. The one first-generation individual from

which the Primus berry is descended was unlike any of the others. But this individual has reproduced true to seed from the beginning.

Rosenberg has shown that in a similar case in the genus *Hieracium* the first-generation hybrids, which are not alike, have different numbers of chromosomes. Presumably, in such cases, the chromosomes of the two species crossed differ so much in habit that they can not function together properly, and some of them are lost in the early cell divisions of the young hybrid. In some individuals, one chromosome is lost, in others other chromosomes are lost; so that, if the supposition here made is true, the young first-generation hybrids do not have the same complement of hereditary characters, which would account for their not being alike.

The fact that these hybrids do not split up in Mendelian fashion in the second and later generations suggests that the corresponding chromosomes in the two sets of chromosomes brought together in these wide crosses are so unlike that they are not drawn together to form bivalents in the reduction division. That is, the reduction division does not occur in the mother cells which produce ovules and pollen. If this should prove to be true, then either of two alternative courses of events would give hybrids which reproduce true to seed without Mendelian splitting.

(1) Seed may be produced parthenogenetically, without the intervention of a reduction division and subsequent fertilization, and this asexual production of seed may continue from generation to generation.

(2) Without a reduction division in the first-generation hybrid, a pollen nucleus may unite with an ovule nucleus, thus giving a nucleus having two sets of chromosomes like the one possessed by the first-generation hybrid. The set of chromosomes in the first-generation hybrid is presumably composed of chromosomes part of which are from one species and part from the other. The double nucleus thus formed will have two sets of chromosomes, every one in one set having an exact duplicate in the other. After this, that is, in the second and later generations, reproduction would take place in the usual manner, without any Mendelian splitting, for the two halves of each bivalent formed in the reduction division would be exactly alike.

It would probably be possible, by cytological study of these constant hybrids, to determine whether the absence of Mendelian splitting is due to either of the causes above suggested.

MUTATIONS.

The term "mutation" has been used and is now used in so many senses that a great deal of confusion has arisen in consequence. Prof. Hugo De Vries, of Holland, after investigating some hundreds

of species of plants, found one species (*Oenothera lamarckiana*) which occasionally produced offspring that were unlike the parent. Some of the new individuals were capable of reproduction true to type. These forms he called mutations. The work of Dr. R. R. Gates, of the University of Chicago, who is making a careful study of the chromosome behavior in these mutants, indicates strongly that these mutations are due to accidents occurring in the reduction division by which chromosomes are either lost or gained or exchanged, so that some of the daughter cells are provided with a set of chromosomes differing from that of the parent species. A good deal of work must yet be done before this matter is settled, and until we know more about it we can not assign mutations of this class to their proper place in heredity and in evolutionary progress.

The term "mutation" has also been applied to any permanent evolutionary change of whatever magnitude or whatever its cause. It is hardly probable that all evolutionary changes are due to accidents in cell division. It would seem rather that most of such changes are due to permanent changes in whatever material is responsible for the development of hereditary characters, and it is probable that we shall ultimately have to make a distinction between these two types of so-called mutations.

LATENCY.

Characters sometimes fail to develop, although present. The reason for such failure may fall into any one of several categories. One of the most important recent papers dealing with this phase of the subject is that of Dr. G. H. Shull in the *American Naturalist*, Volume XLII, July, 1908. The following classification of the different types of latency follows, in the main, Doctor Shull's paper, departures therefrom being noted in the text.

I.—LATENCY DUE TO SEPARATION.

Bateson and his coworkers crossed a cream-colored strain of gillyflowers with a white strain and secured a hybrid which had red flowers. This is explained by assuming that in the cross two characters are brought together which when separated are incapable of producing red flower color, but which when together give rise to this color. Many other breeders have found similar instances, and these characters, which when alone produce no visible effect but when in the presence of other characters give rise to visible manifestations, have been called "cryptomeres" by Prof. E. von Tschermak, a term which is derived from the Greek and which etymologically means "hidden parts." Both von Tschermak and Bateson have shown that purple color in gillyflowers is due to three such cryptomeres. Two of these without the third give rise to the

red color. When the third is present with the first two purple arises. There are other cryptomerer present in gillyflowers which modify these colors, but the numerical relations in their transmission have not yet been fully made out.

Shull found a cryptomeric character in beans in a cross between certain brownish-seeded beans and white-seeded beans. It appears that the white variety carried a cryptomere which when present with the factor which gives rise to the brown color converts the brown into black, thus giving in the hybrid a character which was apparently absent in both of its parents.

In this case we may represent the formula of the two parents as follows:

White parent = $BBpp$.

Brown parent = $bbPP$.

Here B stands for the cryptomere which converts the brown color into black (and which is latent in the absence of P) and P for the producer of the brown pigment. The hybrid would have the formula $BbPp$. The second generation of this hybrid would be as follows:

	B .	P .	pb .		B .	P .	pb .
1 $BBPP$	1			1 $bbPP$	1		
2 $BBPp$	2			2 $bbPp$	2		
1 $BBpp$			1	1 $bbpp$			1
2 $BbPP$	2						
4 $BbPp$	4			16	9	3	4
2 $Bbpp$			2				

The first column in the above table gives the nine types in the second generation of the hybrid, and the figures at the left of the formula show the relative frequency of the types. Thus type $BBPP$ constitutes one-sixteenth of the second generation, type $BBPp$ two-sixteenths, and so on. Since B and P are both present in types $BBPP$, $BBPp$, $BbPP$, and $BbPp$, these four types, constituting together nine-sixteenths of the second generation, will all be black. Types $bbPP$ and $bbPp$ are brown, while types $BBpp$, $Bbpp$, and $bbpp$ will all be white, although two of them have the factor B . The factor B has no effect in the absence of P . We thus have in the second generation of this hybrid 9 blacks, to 3 browns, to 4 whites.

A more complex case of this kind is that of the purple gillyflowers already mentioned. In this case we have to deal with the following factors:

C =one factor of red.

R =other factor of red.

P =the factor for purple.

Of these factors C and R are cryptomeric to each other; that is, neither of them produces a visible effect except in the presence of the other. P is cryptomeric to both C and R . The factor P was

first discovered by crossing a cream-colored variety carrying the factor *C* and a white variety carrying the factors *R* and *P*. The first-generation hybrid was therefore *CcRrPp*. The second generation of this cross gave the following:

	P.	R.	W.		P.	R.	W.
			(or cream).				(or cream).
1 <i>CCRRPP</i>	1	.		2 <i>CcrrPP</i>			2
2 <i>CCRRPp</i>	2			4 <i>CcrrPp</i>			4
1 <i>CCRRpp</i>		1		2 <i>Ccrrpp</i>			2
2 <i>CCRrPP</i>	2			1 <i>ccRRPP</i>			1
4 <i>CCRrPp</i>	4			2 <i>ccRRPp</i>			2
2 <i>CCRrpp</i>		2		1 <i>ccRRpp</i>			1
1 <i>CCrrPP</i>			1	2 <i>ccRrPP</i>			2
2 <i>CCrrPp</i>			2	4 <i>ccRrPp</i>			4
1 <i>CCrrpp</i>			1	2 <i>ccRrpp</i>			2
2 <i>CcRRPP</i>	2			1 <i>ccrrPP</i>			1
4 <i>CcRRPp</i>	4			2 <i>ccrrPp</i>			2
2 <i>CcRRpp</i>		2		1 <i>ccrrpp</i>			1
4 <i>CcRrPP</i>	4						
8 <i>CcRrPp</i>	8			64	27	9	28
4 <i>CcRrpp</i>		4					

This gives in the second generation 27 purples, 9 reds, and 28 whites or creams.

The above illustrations will give the reader an idea of the behavior of cryptomeric characters. These characters are not infrequent, and in the early days when such cases arose they were frequently reported as "exceptions to Mendel's law." Their inheritance is now well understood.

II.—LATENCY DUE TO DOMINANCE OF ABSENCE OVER PRESENCE.

Latency due to dominance of absence over presence was not separately considered by Shull in the paper referred to. Generally speaking, the presence of a character is dominant to its absence, but there are some exceptions. Two of the best known relate to horns in cattle and beards in wheat. We do not know exactly why these characters do not develop when they are in the heterozygote state. It is possible that in both these cases the absence of horns or beards may be due to the presence of some inhibiting factor, in which case the present category of latency would be a simple case of dominance of presence over absence. It seems probable, however, that these characters are simply unable to develop unless represented by two allelomorphs. The reasons for this assumption are rather too abstruse to be given here, for to make them clear would require a great deal of space, and they are also more or less speculative at the present time.^a

^a See article by Shull in *American Naturalist* for July, 1909.

III.—LATENCY DUE TO HOMOZYGOSIS.

This group of facts might perhaps be better described as "patency due to heterozygosis." It includes those cases where a character is patent only in heterozygotes. The following discussion differs in some details from that given by Shull.

In Shull's bean crosses, mottled first-generation hybrids occurred between varieties neither of which was mottled, and subsequent investigation showed that the mottling only occurred in heterozygotes. Tschermak and Locke have both reported similar cases; also Professor Emerson, of the University of Nebraska. In all these cases the mottled beans produce progeny half of which is mottled and the other half not, thus giving a departure from the usual 3:1 ratio found in ordinary Mendelian characters.

The following explanation of all the above cases is here offered. The explanation will be given for mottled character, from which the explanation of the other cases may be easily inferred. The fact that in beans there are mottled varieties which breed true and which when crossed with the new type of mottled beans give ordinary Mendelian phenomena greatly strengthens the hypothesis here stated. Let us suppose that originally the mottling was due to two correlated characters; that is, to two characters which are always transmitted together. We may represent the determiner for this double character as M_c^a . The formula for those strains of mottled beans which reproduce true to type would then be $M_c^a M_c^a$. If we suppose that in some strains of these mottled beans the character a becomes latent or is lost, while in other strains the character c does likewise, while in still others both a and c become latent, we get three types of nonmottled beans, the formulæ for which are $M^a M^a$, $M_c M_c$, and MM . A cross between the first and second of these nonmottled types would give mottling of the character found by Shull. This cross would have the formula $M^a M_c$. In the next generation this would split up into one-fourth $M^a M^a$, one-half $M^a M_c$, and one-fourth $M_c M_c$, in which only the heterozygotes would be mottled, for it is only in them that we have both factors of the mottling. Either of the three types of nonmottled beans crossed with permanently mottled beans would give the ordinary Mendelian behavior of the mottled character in which in the second generation we should have three mottled to one nonmottled.

This same explanation is in accord with the facts in the case of the blue color in Andalusian fowls and the purple color in Imperial primroses. In the case of the blue Andalusians the blue may not be a reversion to a lost character, but may be, in a sense, a new character; but on the above explanation its presence in heterozygotes is assumed to be explicable on exactly the same basis as the presence of mottling in those beans in which it occurs only in heterozygotes.

IV.—LATENCY DUE TO HYPOSTASIS (MASKING).

Sometimes a character may be hidden by the presence of another character which simply obscures it. Thus, in the hair of most species of mammals there are both yellow and black pigments, each of which may be visible because of a certain other factor which causes them to develop more or less in different regions of the same hair. But in the absence of this controlling factor the black and yellow pigments develop in the same regions of the hair and the black thus obscures the yellow. Prof. T. H. Morgan found a case in the cross between the black rat and the Alexandrian rat, in which the black color was dominant over the gray color of the Alexandrian rat, presumably because the black color hid the other color characters.

Characters which are thus obscured by the presence of another character are said to be latent by hypostasis—that is, they are hypostatic to the obscuring character, while the latter is said to be epistatic to the obscured character. These convenient terms were suggested by Professor Bateson. In one of his crosses between black beans and yellow beans Shull obtained some seal-brown beans, and inferred that the seal-brown had been present in the black beans, but was there obscured by hypostasis.

V.—LATENCY DUE TO INHIBITION.

The category of latency due to inhibition is much like the last and was included by Shull, perhaps properly, with it. It seems possible, however, that it may deserve separate treatment. In the cases considered characters have been invisible simply because some other character present obscured them. There are cases, however, where the presence of one character seems to prevent the development of another character. For instance, Prof. V. L. Kellogg, of Leland Stanford Junior University, in crossing certain white and certain colored varieties of silkworms found the white to be dominant. Similar phenomena have been found by Bateson and Davenport in poultry, and the writer, in cooperation with Mr. Q. I. Simpson, has found the same in swine. Here the presence of the white character seems to prevent the color from developing rather than simply to obscure the color. Perhaps we might not be justified in treating this case as anything else than hypostasis. At any rate, the behavior in inheritance is exactly as in the case of hypostasis, as far as the ratios of the various types are concerned.

VI.—LATENCY DUE TO FLUCTUATION.

Some Mendelian characters are highly variable. Shull cites the case of certain leaf lobings which vary greatly under unfavorable conditions, and sometimes entirely fail to develop. When the

plants in question were grown under favorable conditions, it was easy to demonstrate that leaf lobings are a good Mendelian character, but under certain unfavorable conditions the lobing disappears, thus confusing the Mendelian results. Kellogg found a similar case in silkworms. Certain strains of silkworms which produce salmon-colored cocoons when crossed with certain white strains gave results which showed clearly that the salmon color is a Mendelian character. But in some crosses the salmon color became extremely variable, extending all the way from almost pure white to very deep salmon color, thus somewhat obscuring the numerical relations of the colors in the second generation of the hybrid. In some of Correns's work with variegated plants he found a similar character. The variegation, although a good Mendelian character, varied with true green leaves as one extreme, and in some crosses this fact made the number of green leaves in the second generation larger than theory called for.

CORRELATION.

A good many cases have been found where two characters which, so far as appearance goes, are not physiologically related to each other seem always to be transmitted together, and the breeder frequently gets irregular results because of this coupling or correlation of characters. For instance, Tschermak found in Chinese oats that hull-less seed is correlated with long, many-flowered spikelets, and that these two characters were always transmitted together. In Price and Drinkard's work with tomatoes at the Virginia Agricultural Experiment Station they found what seems to be a case of this kind. In one of their crosses one of the parents had green foliage and two-celled fruit. The other parent had yellowish green foliage and many-celled fruit. The hybrid was like the first parent. In the second generation of this hybrid all the plants having green foliage had two-celled fruits, and all those having yellowish green foliage had many-celled fruits, thus indicating that the many-celled condition of the fruit is transmitted with the yellowish green leaf character, at least in this case. Hedrick and Booth, in their work with tomato hybrids, found that dwarf stature was correlated with dark-green rugous leaves, while standard stature was similarly correlated with lighter green smooth leaves.

Such cases sometimes give the breeder a good deal of difficulty. They are of special importance in relation to theories of heredity, and should always be carefully noted and reported.

INDEX.

	Page.
Allelomorphism, definition.....	17
Allelomorphs, characters and determiners of characters in plant breeding.....	17
Andrews, W. A., experiments in propagation of dahlias, and results.....	31
Apple, Baldwin, tree heterozygote in character.....	47
Wealthy, seedlings, study in Canada.....	55
Apples, heterozygote species.....	54
Bacteria, evolution.....	29
Banana, plant vegetatively propagated, producing no seed but retaining vigor..	25
Barber, M. A., study of experimental evolution of yeasts and bacteria.....	29
Barley, individual selection, experiments in Ontario.....	34, 35
Mandscheuri, mass selection in Ontario, experiments and results.....	35
self-fertilized, effect of selection.....	32-33
mass selection, effect on yield.....	34
study of effect of location.....	61-62
Bateson, William, experiments in crossing gillyflowers, and results.....	57, 65-66
investigations of allelomorphism.....	17
study of fowls and the Imperial primrose.....	56
Baur, Erwin, study of white-margined plants.....	62-63
Beans, crossing, experiments and results.....	66-67, 68, 69
hybrid, character.....	56-57, 58
study.....	56
hybrids, mottled, experiments and results.....	68
Berry, Primus, crossing experiments and results.....	63
Booth, studies of tomato hybrids.....	70
Breeding, plant, effect of location on occurrence of variations.....	61-62
relation of evolutionary changes.....	59-61
Bud sports. <i>See</i> Sports, bud.	
Burbank, Luther, experiments in crossing Primus berry.....	63
with poppies in California.....	61
California poppy, selection, results.....	61
Canada, Wealthy, apple, reports of American Breeders' Association.....	55
Carnation, short-lived variety.....	25
Carnegie Institution, experiments in crossing poultry.....	14
Cassava, heterozygote species.....	54, 55
races, study.....	55
Castle, W. E., study of long-eared and short-eared rabbits.....	63
Cattle, crossing, characteristics.....	63
polled and horned varieties, results.....	7-8, 16
Durham, experiments in crossing with Hereford cattle, table.....	18-20
Hereford, experiments in crossing with Durham cattle, table.....	18-20
horns, development and causes.....	67

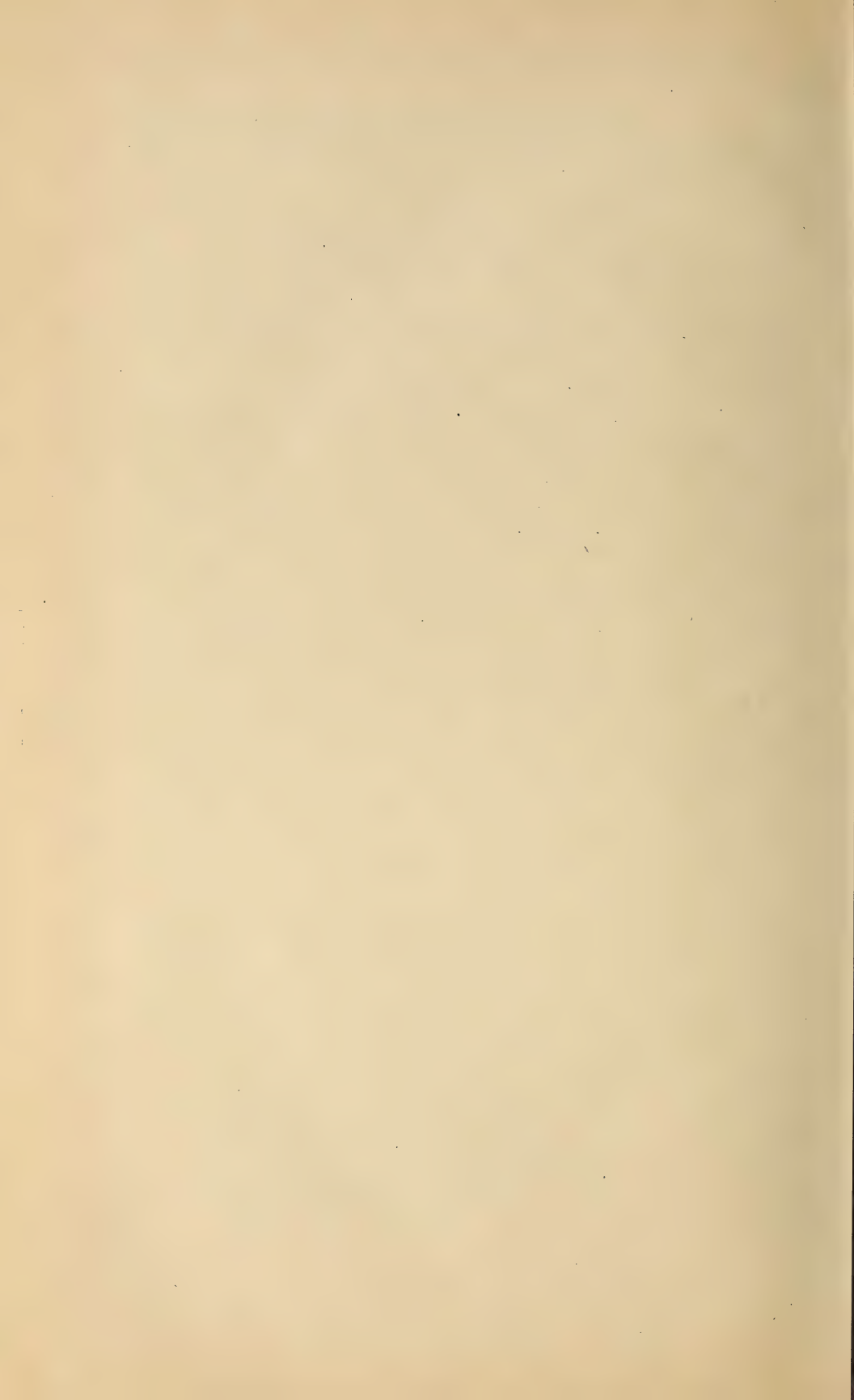
	Page.
Characters of plants, correlation.....	70
fluctuating variations.....	23-25
heterozygote.....	55-58
latency, causes.....	65-70
new, possibility.....	58-59
non-Mendelian.....	62-64
variations resulting from change of location.....	61-62
Cherry, Royal Anne, homozygote species.....	54-55
Chicago University, mutation studies.....	65
Chickens, Barred Plymouth Rock, mating with Indian Game chickens, results.....	14-15
Chromosomes, study of potential elements controlling sexual differences in plant breeding.....	11
Chrysanthemum segetum, selection and results.....	61
Collins, G. N., bulletin entitled "The Importance of Broad Breeding in Corn," reference.....	44
Colorado, potato-growing experiments.....	25
Connecticut, corn-breeding methods, study.....	44
Copenhagen, experiments in breeding beans and barley.....	24
study of effect of seed selection.....	33
Corn, breeding, broad, importance.....	44
experiment station studies in Delaware.....	44
cross-fertilized, effect of selection for high or low ears, table.....	37
on oil and protein content.....	36
selection, results.....	37-46
detasseled, planting, experiments and results.....	46
hybrid, yield.....	55, 56
open-pollinated, breeding and planting methods.....	44-46
seed selection, results.....	44
white, planting alternately with yellow seed.....	45
yellow, planting alternately with white seed.....	45
Cornfield, experiments in fluctuating variations.....	23-25
Correlation of characters of plants.....	70
Corren, study of variegated plants.....	70
Crops, self-fertilized, mass selection.....	33-34
vegetatively propagated, hybridization and selection.....	46-47
Crosses, reciprocal.....	59
Crossing, artificial, selection without.....	26-46
Dahlia, bud variations.....	31
Dandelion, nonfertile, producing seeds and retaining vigor.....	25
Davenport, C. B., studies in poultry crossing.....	14
Delaware, corn breeding, experiment station studies.....	41
De Vries, Hugo, experiments with Chrysanthemum segetum.....	61
study of plant mutations.....	64-65
Dodge, L. G., experiments in seed selection of potatoes.....	31-32
Dominance, principle of heredity in plant breeding, examples.....	7-8
Drinkard, experiments in crossing tomatoes.....	70
East, E. M., methods of corn breeding.....	44, 57
study of fluctuating variations in potatoes.....	26
Emerson, R. A., study of hybrid beans.....	56, 68
England, Cambridge, studies in allelomorphism.....	17
Evolution, plant-breeding changes and their causes.....	59-61
Fluctuation, a cause of latency of characters of plants.....	69-70

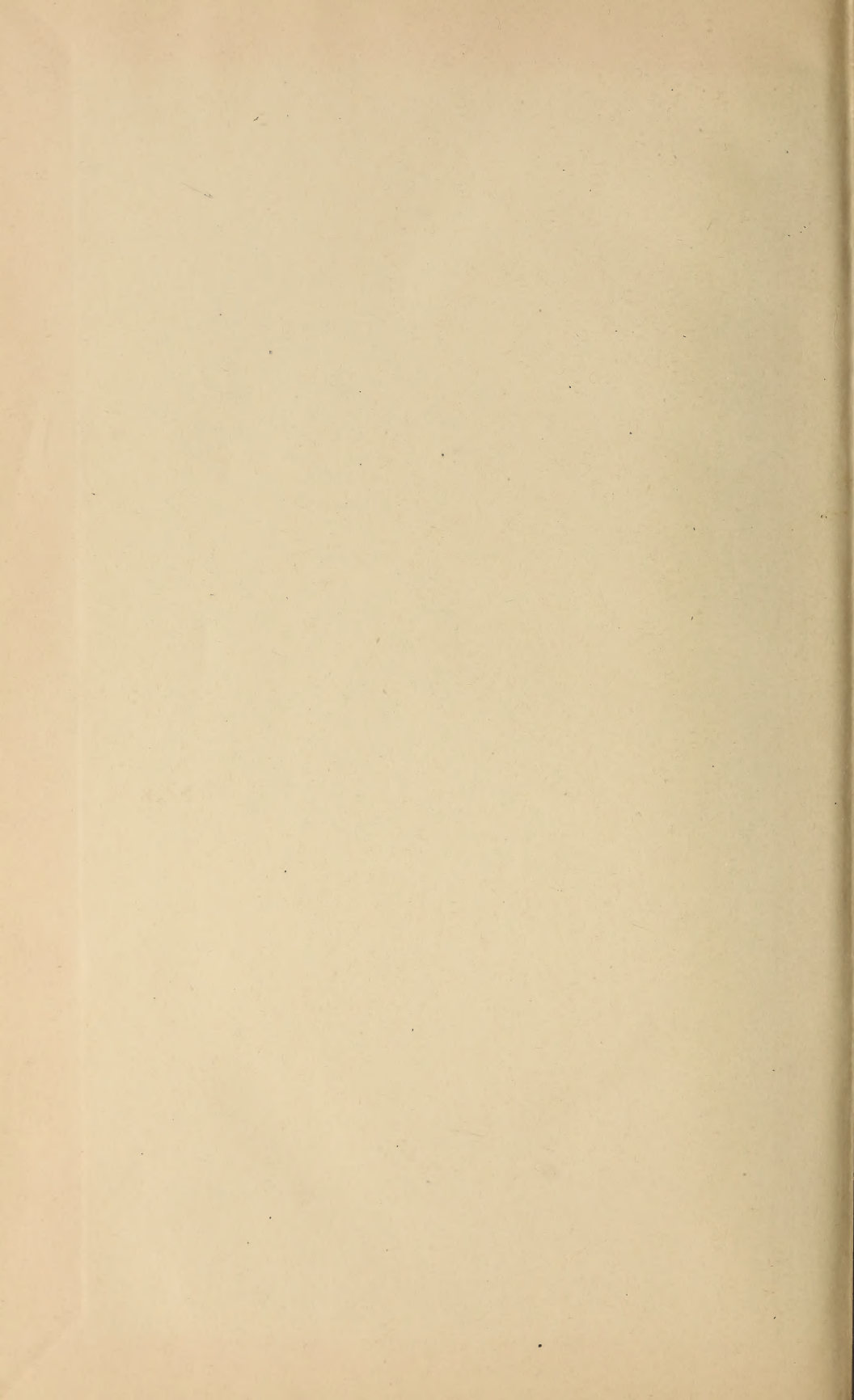
	Page.
Fowls, Andalusian, black, white, and blue, crossing experiments.....	56
color, development and causes.....	68
Bredas, crossing experiments.....	56
crossing, results.....	14-15
Gamete, study of reproductive cell in plant breeding.....	17, 18, 19, 57-58
Gardner, F. B., breeding of corn, recommendations.....	44-45
Gates, R. R., studies of plant mutation.....	65
Germany, Breslau, experiment station studies of rye.....	37
Gillyflowers, crossing experiments and results.....	57, 65-66
Goodale, H. D., study of poultry crossing.....	14-15
Grantham, A. E., studies in seed-corn selection.....	44
Grubb, E. H., maintenance of variety of Peachblow potato in Colorado.....	25
Hanel, Elise, study of evolution of hydra.....	29
Hartley, Charles P., breeding of corn.....	44
Hays, Willet M., experiments in plant selection in Minnesota.....	35-36
Hedrick, studies of tomato hybrids.....	70
Heterozygote characters, study.....	55-58
Hieracium, first-generation hybrid, crossing experiments and results.....	64
Homozygosis, a cause of latency of characters of plants.....	68
Hybridization and selection, cross-fertilized species.....	53-54
self-fertilized species.....	47-53
planting of corn.....	45-48
studies of organism differences in plant breeding.....	11-12
vegetatively propagated crops, advantages and results.....	46-47
Hybrids, hereditary characters.....	64
Hydra, evolution.....	29
Hypostasis, a cause of latency of characters of plants.....	69
Illinois Agricultural Experiment Station, studies in potato growing.....	26
selection of cross-fertilized species.....	36
wheat growing.....	47-48
Indian Game chickens, mating with Barred Plymouth Rock chickens, results..	14-15
Inhibition, a cause of latency of characters of plants.....	69
Introduction to bulletin.....	7
Jennings, H. S., study on unicellular animal paramecium, table.....	26-29, 60
Johannsen, W., experiments in selection of self-fertilized plants.....	33
investigations of fluctuating variations of wheat and barley....	24-25
Kellogg, V. L., experiments in crossing silkworms.....	69-70
Latency of characters of plants, experiments and results.....	65-70
Lawrence, C. W., investigations with hybrid wheats.....	49
Leaf, lobing, study in development and causes.....	69-70
Locke, study of hybrid beans.....	56, 68
London, Genetic Conference, study of effect of seed selection.....	33
Macoun, W. T., study of apple seedlings in Canada.....	55
Maine, studies of selection in plant breeding.....	30
Mammals, color of hair, development and causes.....	69
Mann, Albert, study of effect of location on barley.....	61-62
Mendel, Gregor, discoverer of principles of dominance and recessiveness in plant breeding.....	7
Mendelian analysis of heterozygote races of plants.....	54-55
Morgan, T. H., study in crossing rats.....	69
Morrow, G. E., breeding of corn, recommendations.....	44-45
Mosaics resulting from crossing plants.....	63

	Page.
Mutations, plant, investigations and results.....	64-65
Nebraska, University, study of characters of beans	56
New England, experiments in growing potatoes.....	31
Nilsson, experiments in producing new cereals.....	49
selection of self-fertilized plants.....	24-25, 32-33
studies on evolutionary changes in plant breeding.....	60
study of effect of location on barley.....	61-62
Oats, Chinese, crossing experiments and results.....	70
self-fertilized, effect of selection.....	32-33
mass selection, effect on yield.....	34-35
Oenothera lamarckiana, plant-mutation studies and results.....	64-65
Ontario, Guelph, studies in selection of self-fertilized crops.....	34
Oregon, cherries, growing seedlings.....	54-55
Ovule, study of fertilization germ of hybrid plants.....	9-17
Paramecium, unicellular animal, summary of study on experimental evolution.....	26-29
Pea, garden, crossing two varieties, result.....	7, 8
Pearl, Raymond, study of close-fertilized species of plants.....	30
Pears, heterozygote species.....	54
Pláce effect, variations in characters.....	61-62
Plant breeding. <i>See</i> Breeding, plant.	
Plants, centgener power, result of environmental conditions.....	35
characters, correlation.....	70
heterozygote.....	55-58
latency, causes.....	65-70
new, possibility.....	58-59
non-Mendelian.....	62-64
cross-fertilized, individual selection, effect.....	36-46
problem of improvement.....	43-44
selection and results.....	53-54
experimental evolution, studies.....	26-32
mutations, investigations and results.....	64-65
races, heterozygote, Mendelian analysis.....	54-55
vegetatively propagated and self-fertilized.....	25-26
self-fertilized, effect of selection.....	32-36
individual selection.....	35-36
mass selection.....	33-34
methods of selection.....	33-36
variegated, study.....	70
vegetatively propagated, fluctuating variations due to environment....	26-32
tendency to run out.....	25-26
white-margined, study.....	62-63
Plymouth Rock, Barred, chickens, mating with Indian Game chickens, results.....	14-15
Pollen, diœcious species of plants, use and results.....	59
monœcious species of plants, use and results.....	59
study of fertilization germ of hybrid plants.....	9-17
Poppy, California, selection and results.....	61
Potato, experiments in seed selection.....	31-32
Peachblow, long-lived variety.....	25
Potatoes, bud sports, characters exhibited.....	35
hereditary characteristics and seed selection.....	30, 31-32
seedling, lack of hybridization.....	46
self-fertilized, mass selection, effect on yield.....	34

	Page.
Poultry, crossing.....	14-15, 69
Price, experiments in crossing tomatoes.....	70
Primrose, hybrid, breeding, progeny produced and causes.....	9-17
hybridizing experiments in England, results.....	9
Imperial, color, development and causes.....	68
Propagation, vegetative, fluctuation, effect of environment.....	26-32
Rabbits, long-eared and short-eared, cross, study.....	63
Races of plants, heterozygote, Mendelian analysis.....	54-55
Rats, crossing experiments, development and causes.....	69
Recessiveness, principle of heredity in plant breeding, examples.....	7-8
Recombination, laws and results.....	18-23
Rosenberg, study of Hieracium genus.....	64
Rümker, von, experiments on cross-fertilization of rye.....	37
Rye, cross-fertilization, experiments.....	37
Segregation, natural laws and results.....	8-17
Selection and hybridization, cross-fertilized species.....	53-54
self-fertilized species.....	47-53
vegetatively propagated crops.....	46-47
effect on cross-fertilized species.....	36-46
self-fertilized species.....	32-36
individual, self-fertilized plants.....	35-36
mass, self-fertilized plants.....	33-34
without artificial crossing.....	26-46
Separation, a cause of latency of characters in plants.....	65-66
Shull, G. H., experiments with hybrid corn, results.....	55-58
method of breeding open-pollinated corn.....	44, 46, 55-56
paper on causes of latency of characters of plants.....	65-70
study of hybrid beans.....	56-57
Silkworm, crossing experiments, development and causes.....	69, 70
Simpson, Q. I., studies in crossing swine.....	69
Sorghum, hybrid, evidenced by vegetative vigor.....	55
Species of plants, cross-fertilized, effect of selection.....	36-46
hybridization and selection.....	53-54
self-fertilized, effect of selection.....	32-36
hybridization and selection.....	47-53
Sports, bud, vegetatively propagated.....	30-31, 35
Strawberries, heterozygote species.....	54
Surface, Frank M., study of close-fertilized species of plants.....	30
Sweden, Svalöf, experiments in plant selection.....	25, 32
Swine, crossing, development and causes.....	69
Tomato, hybrids, studies.....	70
Tomatoes, crossing experiments and results.....	70
northern and southern, alternation, results.....	61
study of effect of location.....	61
Tracy, S. M., study of cassava.....	55
W. W., sr., study of transformed tomatoes.....	61
Tschermak, E. von, study of Chinese oats.....	70
hybrid beans.....	56
latency.....	65, 68
Variations in characters of plants, fluctuating.....	23-25
resulting from change of location.....	61-62
Varieties of plants, running out.....	25-26

	Page.
Virginia Agricultural Experiment Station, study of tomatoes.....	22
Waid, C. W., experiments in selection of seed potatoes.....	31-32
Washington Agricultural Experiment Station, studies in crossing wheat.....	20
growing wheat.....	47, 49
of hybrid wheat.....	59
D. C., studies of dahlia by W. A. Andrews.....	31
State, cherries, growing seedlings.....	54-55
eastern, wheat growing, new varieties and total acreage.....	49
Wheat, beards, development and causes.....	67
character, method of determining.....	52
close-fertilized species, varieties selected and experiments in growing..	47-53
crossing bearded and smooth varieties, result.....	7, 16, 17
experiments, Pullman, Wash., results.....	20-23
long-headed and short-headed varieties, results.....	8, 16, 17
experiments in selection of self-fertilized species.....	47-53
field, experiments in fluctuating variations.....	23-25
hybrid, experiments and results.....	47-53, 59
hybridization, method of securing new varieties.....	49
reciprocal crosses, experiments.....	59
self-fertilized species, effect of selection.....	32-33
spring, effect of fall sowing.....	48
type, method of determining.....	52-53
varieties, careful selection as an aid to maintenance of vigor.....	26
winter and spring, effects of crossing.....	50, 52
Wilson, E. B., study of chromosomes.....	11
Yeast, evolution.....	29
Zavitz, C. A., study of mass selection of self-fertilized crops.....	34, 35





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